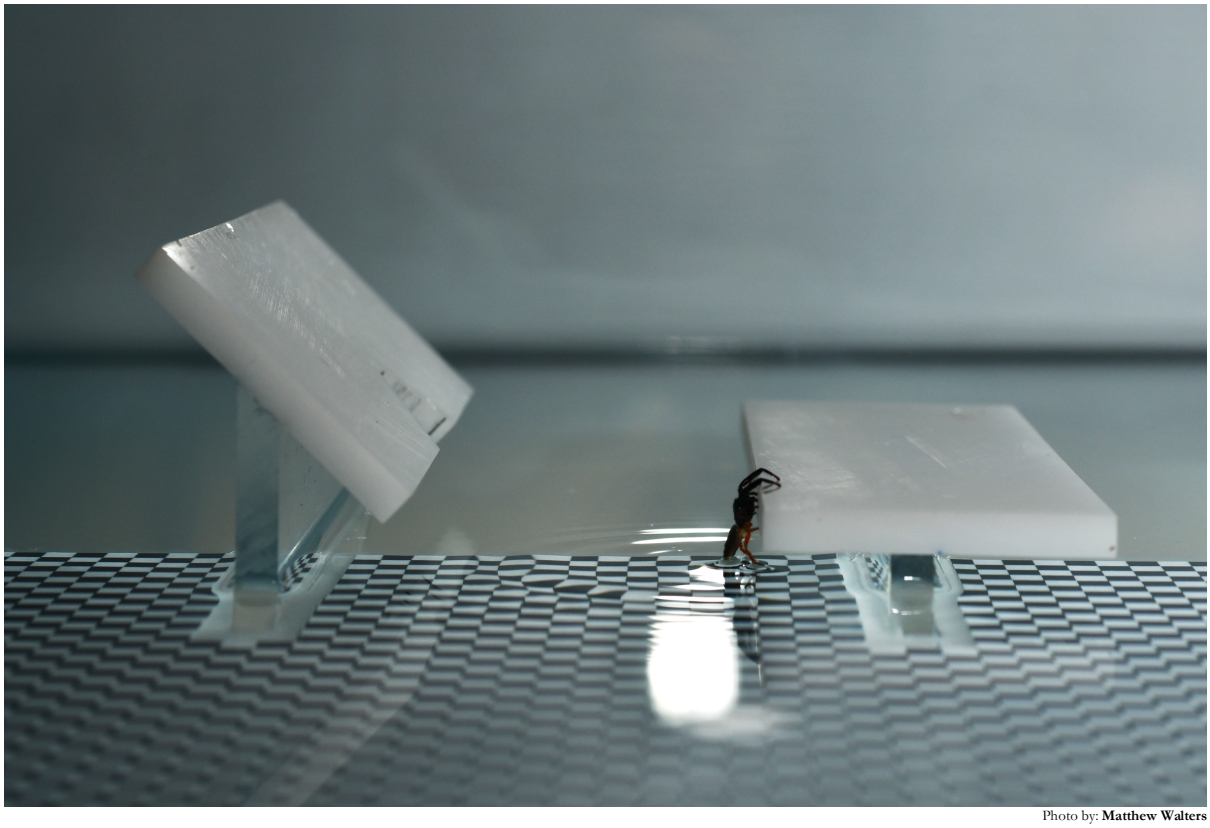
Spatial abilities in jumping spiders



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ABSTRACT

Cognition refers to any state of information processing, including memory, perception, decision-making, and learning. Decision-making, the main component of this thesis, is a cognitive process that allows animals to evaluate their environment so as to avoid less favourable situations. A related process - assessment - is how animals evaluate perceived stimuli, convert these to an informational state, and then infer a specific level of risk or benefit. Both assessment and decision-making are required in navigation, especially in complex 3-dimensional (3D) environments. For example, detouring - the use of indirect routes to reach a goal - in a 3D environment requires spatial memory to remember the location of the goal aimed for. In order to do this, the animal needs to assess its options, because the most efficient route grants energy economy and less time exposed to predators. Finally, the animal must decide which of the multitude of potential routes to take, based on this assessment.

The Clever Foraging Hypothesis (CFH) postulates that individuals have better neurobiological abilities to navigate when living in more complex environments, and some comparative studies on vertebrates have supported this hypothesis. While studies of this in invertebrates are scarce and somewhat inconclusive., spiders from the family Salticidae are excellent candidates to investigate the CFH. Salticids live in a wide variety of habitats with different structural complexity, and their navigational abilities, which include performing complicated detours, are mediated by exceptional vision. In the first section of the thesis, we compared the spatial abilities of three salticid species from environments varying from least to most structurally complex: *Marpissa marina* lives in rocky beaches, *Trite planiceps* inhabits harakeke (New Zealand flax, *Phormium tenax*), and *Portia fimbriata*'s habitat is dense rainforest.

First, in a choice test in which four routes differed in being either short or long and in the presence or absence of a prey item, we investigated route assessment in *T. planiceps* and *M. marina.* We demonstrated that, before detouring, salticids assessed the route and made decisions, although this was cognitively challenging for the studied species. We also demonstrated that the severity of cognitive limitations depended on species, with *M. marina* being less likely to complete any route. We then tested whether *P. fimbriata* and *T. planiceps* could discriminate and assess different routes depending on their length and riskiness to escape from a stressful scenario. Results suggested that while *P. fimbriata* was more likely to choose the easiest and shortest escape routes, *T. planiceps* was faster at both escaping and in its decision-making about the route to take. However, some individuals, particularly among *P. fimbriata,* adopted novel shortcuts instead of the routes expected,

exhibiting a behaviour not before described in salticids. Overall, these findings tentatively support the CFH.

While assessment is the process whereby animals evaluate stimuli, this depends on the perceptual accuracy of the stimuli, and may be improved by the use of multisensory information to reduce ambiguity. The use of multisensory information in predatory or sexually-based behaviours has been previously observed in salticids. However, these have not been extensively studied. In the second section of this thesis, we evaluated perception in salticids in spatial assessment tasks involving risk.

We first evaluated whether *T. planiceps* and *P. fimbriata* accounted for two different sources of stimuli (mechanical and visual cues) to assess a jump. Salticids were initially exposed to either no wind, low wind speed or high wind speeds and were then exposed to intermittent wind. Salticids preferred to jump when there was no wind, and also exhibited slight changes in their pre-jump positioning, depending on wind speed and wind direction. This demonstrates that salticids use not only visual cues, but also mechanosensory ones, when assessing jumps.

Finally, we investigated the use of texture density (the density of the elements of a surface) as a component of visual depth perception cues in experiments with, and without, optical illusions. Initially, spiders were given the choice to jump over an illusion resembling a trench or over a control visual pattern (similar texture but without the illusion). We then exposed spiders to an arena with two areas under which there were equivalent checkerboard substrates: one was a low drop and another was a high drop (cliff experiment). We then presented them in an arena in which both areas were of the same height but the substrate had different texture densities, simulating a low or high drop. In a last experiment, we controlled for some binocular and monocular depth perception mechanisms to try to ascertain the mechanism used by spiders for absolute depth perception. Here, we demonstrated that *T. planiceps*, although not fooled by the optical illusions, uses texture density to certain extent as a depth perception cue. From this, we can confirm that salticids use a monocular depth perception mechanism to estimate absolute distance, but this does not preclude the possible use of some binocular mechanisms.

Overall, this work has provided significant insights into the cognitive and perceptual capabilities of salticids, and provides several avenues for further research into the 'brains' of these fascinating tiny animals.

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CHAPTER ONE. Introduction

Trite planiceps, also known as the 'black-headed jumping spider'.

Cognition refers to any state of information processing (Dukas 2002), including memory, perception, decision-making, and learning (Shettleworth 2010). More descriptively, cognition implies at least four steps: 1) obtaining information from the environment (perception), 2) processing that information, 3) retaining the information, and 4) deciding to act according to it (Shettleworth 2010). Neural integration processes are diverse and show different qualities across taxa. Cognitive abilities differ as a consequence of adaptations to the specific demands provided by the habitat used by each species (Menzel 2013). Therefore, cognition involves a diverse range of mechanisms, from the most basic type of learning (habituation), as that found in marine molluscs, such as *Aplysia*, with simple nervous systems (Castellucci et al. 1970), to social learning and episodic-like memory, such as that found, for example, in primates (Menzel 1999, 2005, Reader & Laland 2002, Schwartz et al. 2004, Reader et al. 2011).

Nevertheless, "no behaviour is strictly learned or entirely innate" (Shettleworth 2010). Instead, behaviours are the consequence of inherited traits depending on the population's genome forming part of the animal's genotype (Shettleworth 2010). Thus, innate behaviour is dominated by inherited traits, requires little internal processing, and changes relatively little with experience. In contrast, experience-based behaviours can be innately triggered but are modified or adjusted depending on experience and interaction with the environment (Menzel 2013).

Cognition determines behavioural traits that affect an animal's ecology and evolution (Dukas 2004), but cognitive abilities are simultaneously affected by a combination of genetic and environmental factors (Richards 1987, Plomin et al. 2013). Factors that are known to affect cognitive capacity include brain size (Krebs et al. 1989, Sherry et al. 1989, Krebs 1990, Reader & Laland 2002, Overington et al. 2009, Sol 2009), individual genetic variation (Mery & Kawecki 2002, Mery 2013), foraging strategy (Falk et al. 1992, Shettleworth 1993), habitat type, and the level of sociality in the species (Joffe & Dunbar 1997, Barton 1999, Reader et al. 2011).

Although genetic factors influence the cognitive ability of a species, environmental components are also important (van Praag et al. 2000), and can swamp the genetic basis of cognition (Rampon et al. 2000, Mery 2013): individuals who can learn to rapidly adapt to changes in their environment are expected to reap fitness benefits (Chittka et al. 2012).

Furthermore, the structural complexity of the environment inhabited by the species can considerably affect its cognition. Clarin and colleagues (2013) found that three species of *Myotis* bats have different learning capabilities depending on the complexity of the environment in which they usually forage. They observed that bats that forage in complex and less predictable habitats tend to perform better in complex-rule learning tasks than bats that forage in simpler and more predictable environments. Additionally, studies show that environmental complexity can directly

affect the cognitive capacity of individuals of the same species during development – a phenomenon known as developmental plasticity (Kasumovic 2013). In jumping spiders (Salticidae), Liedtke and Schneider (2017) found significantly higher learning abilities in individuals reared in social environments compared with spiders raised in isolation. Likewise, salticids are more exploratory when reared in enriched environments compared to those reared in empty cages (Carducci & Jakob 2000, Liedtke et al. 2015).

Why is there variation in cognition?

There have been several suggested hypotheses to try to explain the evolution of cognition (and interspecific differences in cognition), as a consequence of a specific selection pressure factor that has shaped behaviour (e.g. epiphenomenal, ecological, and developmental factors, see Dunbar 1998).

In primates, the existing, but still controversial (Chittka & Niven 2009), link between brain size and cognitive capacity (Reader et al. 2011) may be caused by social interactions. Specifically, data demonstrates that primates that show a wider range of complex behaviour and higher-order cognitive ability possess greater neocortex volume, which is also related to group size. The Social Brain Hypothesis (SBH) suggests that animals that form big groups impose constraints on information-processing, favouring brain development to manage complex relationships within group members (Dunbar 1992, 1998). Such complex relationships in primates include the recognition and interpretation of visual signals, memory for face recognition, ability to process emotional information, tactical deception, etc. (Dunbar 1998). The SBH has been corroborated not only in primates, but in bats (Barton & Dunbar 1997), carnivores (Gittleman 1986, Barton & Dunbar 1997, Dunbar & Bever 1998, but see Finarelli & Flynn 2009), and insectivores (Dunbar & Bever 1998) and potentially in odontocete cetaceans (Marino 1996). In birds, even though brain size and group size are not correlated, there is a correlation between the level of pairbonding with relative brain size. Shultz and Dunbar (2007) argue that here a similar mechanism as the SBH is happening, in terms of interaction complexity: the complexity of the pairbond relationship (e.g., behaviour sincronization, long-term relationships, etc.) has created constrains that favoured the development of a larger brain (Dunbar 2009).

However, the SBH fails to predict the distribution of brain/group size relationship in several vertebrate taxa (Byrne 1997, Beauchamp & Fernandez-Juricic 2004, Schulz & Dunbar 2006, 2007, Finarelli & Flynn 2009, Maclean et al. 2009) and is not applicable in insects. In insects, social species seem to have more limited cognitive ability than solitary species (Chittka & Niven 2009, Farris 2016), presumably because individuals of eusocial species have a limited range of

behaviours due to division of labour, whereas solitary species perform a wider range of behaviours (Farris 2016).

The 'Ecological Intelligence Hypothesis' proposes that ecological factors create constraints that affect animal cognition (Milton 1981, Sol et al. 2005, Sol 2009, Rosati 2017). Such constraints can be dietary, including the complex spatiotemporal distribution of foods and the use of extractive foraging techniques ('Extractive Foraging Hypothesis'), or responses to a fluctuating environment (Clutton-Brock & Harvey 1980, Rosati 2017).

In birds, foraging behaviour is believed to be the dominant driving-force for the evolution of cognitive ability (Krebs 1990). The 'Adaptive Specialization Hypothesis' (Pravosudov & Roth 2013), proposes that the need for caching food for survival in certain bird species was the principal ecological factor that contributed to an enhancement of spatial memory and its underlying neural mechanisms (Krebs et al. 1989, Krebs 1990, Sherry et al. 1989). The area of the brain critical for spatial memory in birds is the hippocampus (Krushinskaya 1966, Sherry & Vaccarino 1989, Hampton & Shettleworth 1996), and food-caching species have larger hippocampal volume, longer memory retention, and better spatial memory than non-caching species (Krebs et al. 1989, Sherry et al. 1989, Biegler et al. 2001, Pravosudov & Roth 2013).

A variant of this hypothesis is the 'Spatial Cognition Hypothesis' (Barton & Dunbar 1997), which is related to the 'Foraging Niche Hypothesis'. These explain, correspondingly, the effect of home range size and the distribution of available food on cognitive ability (Clutton-Brock & Harvey 1980). The premise is that frugivorous species require good spatial memory for the location of food patches and perhaps an ability to estimate travel routes between them, particularly in spcies with large home range sizes (Clutton-Brock & Harvey 1980). While folivorous species depend on a food source that is densely distributed, and is more predictable in time and space (Clutton-Brock & Harvey 1977), species with food that is patchily distributed and with bigger home range would present better cognitive abilities than those whith a more homogeneous food distribution and small home range (Harvey & Krebs 1990, Clutton-Brock & Harvey 1980). This has been observed in comparative studies. For example, frugivorous bats have larger brains than insectivorous bats (Pirlot & Stephan 1970, Eisenberg & Wilson 1978, Stephan et al. 1981), while folivorous primates have smaller brains than frugivorous-omnivorous primates (Clutton-Brock & Harvey 1980, Harvey et al. 1980, Mace et al. 1981), and folivoros rodents have both smaller brains than non-folivoros rodents, and larger home ranges (Harvey et al. 1980).

Finally, another hypothesis related to, and perhaps derived from, the Ecological Intelligence Hypothesis is the Clever Foraging Hypothesis (CFH). The CFH postulates that individuals have better neurobiological abilities to navigate when living in more complex

environments (Parker & Gibson 1977, Striedter 2005, Park & Bell 2010), and evidence that support it is found in both vertebrate and invertebrate taxa. For example, rats and mice perform better in spatial memory tasks when they are housed in enriched environments (Nilsson et al. 1999, Williams et al. 2001, Frick & Fernandez 2003, Frick et al. 2003), and wild mole-rats (*Cryptomys hottentotus natalensis*) from complex natural environments have better spatial cognitive performance than mole-rats raised in a simple laboratory environment (du Toit et al. 2012). Additionally, the Damaraland mole-rat (*Fukomys damarensis*), that lives in complex burrow systems, has superior spatial abilities (higher memory retention and faster spatial learning) compared with the Cape mole-rat (*Georychus capensis*), which lives in simpler burrow systems (Costanzo et al. 2009). Comparative studies evaluating the morphology underpinning spatial ability in relation to environmental complexity also support the CFH. An association between environmental complexity and telencephalon morphology, which is responsible for spatial memory and navigation tasks, has been observed in fish (Bauchot et al. 1977, Striedter 2005, Park & Bell 2010; but see Ahmed et al. 2017). Similarly, Safi & Deckman (2005) found a correlation between hippocampus size (responsible for spatial memory) and environmental complexity in different bat species, with hippocampus size increasing with incrementing environmental complexity. In desert ants, navigational abilities are more strongly influenced by environmental complexity than phylogenetic relatedness. *Melophorus bagoti*, which inhabits in a visually-rich semi-desertic environment with tussocks, shrubs and rocks, relies more on visual landmarks to orient than *Melophorus* sp. and *Cataglyphis fortis*, which live in visually-barren environments (salt-pans; Schwarz & Cheng 2010, Schultheiss et al. 2016). Besides being closely related, *M. bagoti* and *Melophorus* sp. also have different navigation behaviour (Schultheiss et al. 2016). By relying more on path integration (navigation mechanism based on idiothetic cues, see below) than on visual cues, the behaviour of *Melophorus* sp. is more similar to that of *C. fortis* than *M. bagoti* (Cheng et al. 2006, Narendra et al. 2007, Schultheiss et al. 2013). Furthermore, intra-specific differences have been observed in *M. bagoti*: in uncommon cases in which colonies of are located in areas without beacons, these individuals in such unusual conditions rely more on path integration than on visual cues (Narendra 2007, Cheng et al. 2012). Schwarz & Cheng (2010) suggest that natural selection could have determined the capacity of each ant species to rely on each navigation mechanism depending on the characteristics of the environment. Nevertheless, comparative studies on spatial abilities depending on environmental complexity in invertebrates are scarce.

Studies in salticids have proven that, as in bees and ants, spiders also perform complex spatial tasks, which makes them ideal candidates to evaluate cognitive abilities and make inter-specific comparisons. Attempts to compare cognitive abilities among spider species are rare

(Eberhard 2007, Eberhard & Wcislo 2011) and inconclusive. An the scarce number of comparative studies in salticid cognition (Tarsitano & Jackson 1992, 1994, Cross & Jackson 2016) suggest that the cognitive abilities are graded. However, the effect of the environmental complexity on spatial abilities in spiders has not yet been studied, which makes a starting point to test the CFH in this family.

Our main objective of this thesis was to explore different aspects of spatial cognition in jumping spiders through a series of comparative studies that cotributed to the idea of intra-specific differences in cognition and that shed light on the validity of the CFH. By no means this is a work that tested the CFH, but rather that provided data towards this hypothesis.

Jumping spiders (Araneae: Salticidae)

The family Salticidae is the largest in the order Araneae, containing 7635 described species (World Spider Catalog 2019). Jumping spiders (as commonly named) are characterised by a pair of large forward-facing anterior-medial eyes (AME), a typically stout body and short legs (Robinson 2005). Salticids are wandering predators that do not build webs to catch prey. Instead, like felines, they visually locate and approach their prey slowly, attacking by pouncing on the prey from an appropriate distance (Foelix 2011). Salticids are active during daylight (Tork 2018) and return to their silk cocoon-like nest during the night. Apart from jumping easily, either to catch prey or to move across a gap, their most outstanding attribute is vision. Salticid behaviour is rather complex, and a wide range of studies support the existence of multiple cognitive abilities, mainly enabled by their visual prowess (e.g., Skow & Jakob 2005, Jakob et al. 2007, 2011, Jackson & Cross 2011, Cross & Jackson 2016).

Spatial abilities in salticids

Central foragers are animals that move from a central point (e.g., burrow, nest) to forage or find a mate (Ortega-Escobar 2006). In Hymenopterans (e.g., wasps, bees, and ants) the individuals rely on a set of different cues and mechanisms to find their way back to this central point. One of the most frequently used mechanisms is path integration (Papi 1992): an internal representation of the position of the individual with respect of a specific point. Such mechanism maintains a frequent update of the distance and direction of the animal and gives the advantage of moving towards the path integration coordinates of a known point (Collet & Graham 2004). Thus, desert ants are able to return to the nest in a straight line after finding food. Moreover, other

mechanisms, such as the use of landmarks, allow these insects to calibrate their path integrator and ensure their orientation with respect to known points (e.g., nest, feeder).

Path integration has also been observed in some spiders, such as lycosids, the funnel web spider (*Agelena labyrinthica*), the nocturnal ctenid spider (*Cupiennius salei*), and the namib desert spider (*Leucorchestris arenicola*). These species use path intergraton to return to their burrows (Seyfarth et al. 1982, Görner & Claas 1985, Ortega-Escobar 2002, Nørgaard et al. 2003).

Salticids commonly live in complex three-dimensional environments and they normally come back to their nest (Jackson 1979, Mooney & Haloin 2009) by using visual cues or beacons (Hoefler & Jakob 2006). Due to it is unlikely that use stereotyped paths, salticids need to constantly make decisions about routes leading towards a specific goal (e.g., prey, nest, mate). These decisions are directly related to the individual's fitness, as an incorrect route translates into more time exposed to predators, more energy loss (Gibson et al. 2007), or, when the aim is a prey item, a missed opportunity for a meal.

Furthermore, due to habitat characteristics, rather than walking a straight line, salticids are sometimes forced to take detours, defined as an indirect route taken by an animal when the direct route is blocked (Jakob et al. 2011), in order to reach the goal. Several salticid species have been demonstrated to take detours to have access to prey (Tarsitano & Jackson 1992, 1994, Cross & Jackson 2016), which suggests that making detours is a common behaviour in this family.

Detouring is an elaborate cognitive process, as it implies route planning after scanning several possible alternatives (Cheng 2016). Detours can consist of several components; for example, climbing down a branch that is connected to a leaf on which the prey lies. Here, spiders not only have to remember the relative position of the primary objective (prey), but also the selection of an access route involving secondary objectives (the branch). In moving towards a secondary objective, the spider commonly turns away from the position of the target prey, and therefore must retain a memory or internal representation of the relative position (location) of that prey at all times (Hill 1979, Tarsitano & Jackson 1992, Tarsitano & Andrew 1999, Tarsitano 2006). Sometimes, after moving towards the detour the salticid performs a series of 're-orientations' in order to keep track of the primary objective (Hill 1979). Upon reaching the secondary objective, the spider focuses its attention on the next objective that will bring it closer to its goal (Hill 1979). Moreover, Hill (2007) suggested the use of tertiary, and even possible quaternary, objectives in salticids, depending on the complexity of the detour.

Re-orientations are fast and very precise: the cephalothorax turns the precise angle required so that the AME point towards the objective, without apparent error. This internal representation of the prey's location and its calibration, along with the spider's displacement has been interpreted

as evidence of path integration (Hill 2007), although technically as this is not with respect to a central place, this does not satisfy the criteara commonly applied for path integration.

Previous studies have documented salticid detouring behaviour (Hill 1979, Jackson & Wilcox 1993). From studies in nature and in the laboratory, we now know that salticids can solve tasks that suggest the ability to: a) remember the position of the objective from the beginning of the detour, b) use detours that initially take the spider away from the goal, and c) assess which detour leads, and which do not lead, to the desired objective (Tarsitano & Jackson 1997, Cross & Jackson 2016, 2019). However, there is no information about what features of a detour are actually taken into account in order to be followed. In other words, when different routes lead to an objective, are more efficient routes being identified and preferred by the spiders?

I centred the study in **Chapter 2** on salticid detouring in light of the CFH (Clever Foraging Hypothesis). This is a comparative study in which we evaluated the ability of two species from different environments (rocky shore vs harakeke | New Zealand flax, *Phormium tenax*) to identify and assess the most efficient route leading towards prey. Although the routes were not as intricate as in other studies (e.g., Tarsitano & Jackson 1997, Cross & Jackson 2016), the task was cognitively demanding for the spiders in terms of decision-making and spatial memory. This was because the spiders had to choose one out of four (rather than the usual two in other studies) routes that varied both in length and in leading or not leading to prey. Additionally, visual access to prey was available only at the beginning of the route (as in Tarsitano & Jackson 1997). In this study, we used *Trite planiceps* Simon and *Marpissa marina* Goyen*,* species thought to have more limited spatial capabilities than *Portia*, the salticid equivalent of Einstein and therefore heavily studied in detour tasks. Specifically, we wanted to determine: 1) if salticids are able to decide on a route during the scanning phase before embarking on a route, and remember this even after the goal is visually blocked; 2) if salticids prefer short routes over long routes; 3) if there are species-specific differences in spatial ability. Correspondingly, the first hypothesis was that spiders would be able to remember the goals' position even though the spiders could only see it at the beginning of the trial. Our second hypothesis was that spiders would be able to assess the most effective route (short and with prey) out of four different options. Finally, we hypothesised that *Trite planiceps* would outperform *Marpissa marina*, because it inhabits a three-dimensionally more complex habitat, thus potentially having better spatial abilities.

The exceptional case of *Portia*

The salticid genus *Portia* is classified within the subfamily Spartaeinae (Maddison et al. 2014) which specialises on preying on other spiders (Cross & Jackson 2016). The genus *Portia*

currently comprises 17 species which live in very complex three-dimensional rainforest habitats in which they prey upon different spider species (Jackson & Blest 1982, Jackson & Wilcox 1990, Harland & Jackson 2000, 2001). This genus has been described as the spider group with the most complex behaviour due to their outstanding cognitive ability and behavioural flexibility (Jackson & Pollard 1996, Jackson & Cross 2011). This 'jack-of-all-trades, master of all', as *Portia* is referred to by Jackson & Hallas (1986), uses specific strategies to hunt each one of its wide variety of spider prey. From entering a web in order to eat the spider in its own web (Cerveira et al. 2003), to avoiding attacking spitting spiders from the front where they can be in range of the sticky defensive spit – or indeed choosing to hunt spitting spiders holding eggs sacs in their mouths (Jackson et al. 2002, Li & Jackson 2003), *Portia*'s incredible predatory flexibility and specialisation has not been found in other spiders. *Portia*'s spatial abilities are also surprising, being characterised with having scanning phases which allow them to plan a detour ahead of time and choose the best route option to reach a goal (Tarsitano & Jackson 1992, Jackson & Wilcox 1993, Tarsitano & Andrew 1999, Tarsitano 2006, Cross & Jackson 2016). Detours can be over 127 cm long, and the spider can be out of sight from its prey for > 80 min in nature (Jackson & Wilcox 1993), implying not only an outstanding sense of orientation in three-dimensional space, but, due to the spider's need to move away from the prey's position to follow the detour, also acute spatial memory.

Other invertebrate examples of skilful spatial abilities are found in bees and ants. Bees are able to memorise and recognise landmarks near the goal by their physical features (size, shape, and colour) in order to locate their destination (von Frisch 1967, Gould 1987). Bees can also use the pictorial representation of landmarks surrounding their goal in order to pinpoint its exact location (Wehner & Menzel 1990), remembering these for a long period of time. Additionally, bees are able to integrate information about vectors taken in a flight to successfully orient and come back to the colony or a food source (Cartwright & Collett 1983), allowing them to make novel shortcuts, even if they cannot see the goal (Menzel et al. 2005, Menzel et al. 2011). Desert ants can return to their nest in a straight line (a shortcut) by using path integration (an internal navigation mechanism that registers turns, direction and steps by the ant), even if that was not the outbound route. Shortcutting in ants is achieved by arithmetic calculations of the vectors already performed by the ant, and is commonly linked to a visual landmark or beacon (Wenher & Wenher 1990).

The ability of a bee to conduct a foraging expedition may be compared with the ability of a salticid to conduct a detour to reach a goal: in each case, visual information is a significant determinant of the immediate direction of movement, and memory of the relative location of a 'primary objective' (either the location of the colony, or of prey, respectively) must be constantly mentally updated as a consequence of the animal's movement (Hill 1979).

In contrast to primate evolutionary history, which, in the more recent lineages (including humans), evolved favouring cognition complexity (Byrne 2000), salticids have evolved differently. In salticids, the subfamily Spartaeinae, known to be one of the most ancestral of the family (Wanless 1978, 1984, Blest 1983), comprises the genus *Portia*: by far the genus with the most complex cognition in the family (Jackson & Cross 2011). The explanation for its outstanding cognitive ability has not yet been answered. However, *Portia*'s habitat and preference for dangerous prey (spiders can kill *Portia*) requires them making complex detours to reach the prey and often walking through the prey spider's web (Jackson & Hallas 1986, Jackson & Wilcox 1993). Based on the CFH, we believe that it is possible that the environmental complexity in which *Portia* lives has caused enough selective pressure to shape its extreme behavioural complexity and flexibility.

Chapter 3 is a comparative study between *Portia fimbriata* Doleschall and *Trite planiceps*. Here, we tested route assessment in a different scenario from the traditional continuous route setup (e.g., **Chapter 2**, Tarsitano & Jackson 1992, 1994, 1997; Tarsitano & Andrew 1999; Tarsitano 2006). Based on the premise that salticids avoid water, we provided spiders with available routes to escape from a pool. These tests demanded two types of distance assessment, the length of the route, and the length between the gaps of the discontinuous routes. The main objectives were 1) To determine if salticids can a priori assess route distance and riskiness; and 2) To determine if performance is related to the species' environmental complexity, age, and sex. Our first hypothesis was that *Portia fimbriata* would be more effective at making efficient route choices compared to a salticid from a less complex habitat and not known for exceptional cognitive ability, *Trite planiceps*. As salticid performance improves with knowledge about the environment (Edwards & Jackson 1994, Aguilar-Arguello et al. 2018), we also predicted that adults would outperform subadults. Our last hypothesis was that females would outperform males, as these have shown to be more motivated during predation and learning tasks (Jackson & Wilcox 1990, Jackson & Pollard 1996, Jakob & Long 2016).

Risk assessment

To solve problems, animals can either have cognitive processes that allow them to evaluate the costs and benefits of certain behaviour or decision (use of declarative knowledge), or they can simply follow a 'rule of thumb' (use of procedural knowledge) that does not necessitate decision-making. Decision-making is an important cognitive process that allows animals to evaluate their environment so they can avoid less favourable situations. In contrast to procedural knowledge mechanisms, decision-making allows animals to adapt and to adjust to unpredictable environmental changes. Examples of decision-making include choosing mates (Bateson 1983),

selecting a place to live (Partridge 1978), and where to forage (Stephens & Krebs 1986). A related process - assessment - is how animals evaluate perceived stimuli, convert these to an informational state, and then infer a specific level of risk or benefit (Blumstein & Bouskila 1996). Therefore, decision-making is the cognitive process that occurs between assessment and an observable behaviour (Blumstein & Bouskila 1996).

Assessment in vertebrates has been well-documented and includes assessment of mate quality (Halliday 1983, Dick & Elwood 1989), patch quality (Stephens & Krebs 1986), resource holding potential (Riechert 1982, Dowds & Elwood 1983), and predation risk (Lima & Dill 1990, Bouskila & Blumstein 1992), among others. Assessment of predation entails another important component: risk. Survival depends greatly on the capacity of an organism to avoid biologically-dangerous situations. Therefore, the avoidance of danger requires the ability to discriminate between - and make decisions about - stimuli that could be harmful from stimuli that signify harmless or beneficial situations (Schiff et al. 1962). For example, in the context of predation, some vertebrates are able to assess the risk of being preyed upon according to predator distance, the proximity to their own refuge, the approaching speed of the predator, and the number of nearby conspecifics (Stankowich & Blumstein 2005).

Finally, decision-making and assessment can be informed not only by the use of one sensory modality but by multisensory information (Sih 1992, Dall & Johnstone 2002, Dall et al. 2005), sometimes enhancing the response of the organism (Partan & Marler 1999, Partan et al. 2009, Smith & Belk 2001). The use of multisensory cues on decision-making has been shown in assessment of predation risk (e.g., mosquitofish, *Gambusia affinis*: Smith & Belk 2001, Ward & Mehner 2010; crabs, *Heterozius rotundifrons*: Hazlett & McLay 2005; grey squirrels, *Sciurus carolinensis* Partan et al. 2009; roach fish, *Rutilus rutilus*: Martin et al. 2010), communication (e.g., ants: Hölldobler 1999), and interactions with abiotic aspects of the environment (e.g., butterflies, *Callophrys*: Johnson & Borgo 1976), among others.

In arachnids, the use of multisensory cues to make decisions is not new: whip spiders (Amblypygi) use both olfactory and visual cues for homing (Hebets et al. 2014). Female wolf spiders (Lycosidae) respond to males through perception of seismic and visual stimuli (Hebets & Uetz 1999, 2000, Uetz & Roberts 2002, Hebets & Papaj 2005, Roberts et al. 2006), and males have more chances to be chosen as a mate if they use both modalities during courtship compared with one (Hebets & Uetz 2000). Additionally, lycosids are able to visually assess patches with different prey density, choosing patches with higher prey density over those with less prey (Persons & Uetz 1998). Among salticids there are also well-documented cases, such as those of *Evarcha culicivora* and of *Portia,* described below.

Evarcha culicivora is a specialised salticid that preferentially feeds on blood-fed female *Anopheles* mosquitoes. By using visual and odour cues (Jackson et al. 2005, Cross & Jackson 2009) *E. culicivora* can discriminate among several types of visually-similar prey: non-*Anopheles* mosquitoes, male *Anopheles* mosquitoes, and even female *Anopheles* that have, and have not, fed on blood (Jackson et al. 2005, Nelson & Jackson 2006, 2012a). Prey preference and the predation strategy of these spiders is innate (Nelson et al. 2005). However, prey preference varies with the prior feeding condition: sated adult *E. culicivora* chooses *Anopheles* over *Culex* mosquitoes, and prefers sugar-fed female *Anopheles* over male *Anopheles* (Nelson & Jackson 2012b). In addition, *E. culicivora* is able to feed on prey of a specific size in relation to its own size (big spiders attack bigger mosquito prey, whereas juvenile spiders tend to attack smaller mosquito prey; Nelson et al. 2005). Regarding *E. culicivora*'s predatory strategies, juveniles innately prey upon *Anopheles* mosquitoes with a juvenile-specific strategy which consists of approaching the mosquito from behind, creeping under it, and biting underneath the thorax (Nelson et al. 2005). Once bitten, the mosquito flies away, with the spider on it, until the venom acts and the mosquito lands again, whereupon the spider begins eating. Selection of *Anopheles* over *Culex* and attacking at the exact body part is crucial, as the spider attaches safely to the flying mosquito only under these conditions. Nevertheless, adults lose this specific predatory strategy, and simply pounce on the mosquito, as they weigh enough to stop it from flying away (Nelson et al. 2005). This predatory behaviour suggests an example of procedural knowledge mechanism in juveniles, but flexibility in prey preference at all ages suggests prey assessment involving decision-making according to hunger level and experience.

The second case is found in *Portia labiata*, which can also evaluate the risk of dangerous prey. Spitting spiders (*Scytodes* sp.) are dangerous because they launch a sticky substance ('spit') from their mouths for both defence and predation. *Portia labiata* can become *Scytodes*' prey. However, Li and Jackson (2003) observed that *P. labiata* is able to discriminate non-dangerous female *Scytodes* carrying eggsacs in their mouthparts (which prevents them from spitting) from a dangerous female without an eggsac, preferentially attacking *Scytodes* according to their risk of being harmed (i.e., attacking eggsac-carrying *Scytodes*).

In **Chapter 4**, we studied the use of multisensory information involved in risk assessment in two salticid species while performing a targeted jump with the presence of wind. Our aim was to determine if salticids are able to assess a jump by taking into account not only the visual information enabling the precise location of the landing point, but also the presence, speed, and direction of wind that could affect the characteristics of the jump. We hypothesised that salticids would perform targeted jumps differently according to the presence and speed of the wind in three aspects: 1) Changing its trajectory, being flatter as the wind increases. 2) Changing its positioning

with respect to wind direction. 3) Jumping downwind in order to favour the jump instead of 'fighting against' the wind. Using two species, *Portia fimbriata* and *Trite planiceps* we also hypothesised that *Portia* would outperform *Trite*. Finally, we predicted that, in an intermittent wind condition, spiders would tend to jump during periods without wind.

Visual perception in salticids

Salticids are one of the most visually-guided animals known (Land 1969a). Unlike other spider families, salticids rely heavily on vision to perform activities such as predation, navigation, and courtship. Salticids have four pairs of eyes, having a visual field almost covering 360º. Of the eight eyes, six of these are called secondary eyes, despite the fact that perceive high-resolution images (from 0.4º to 2º, Land & Fernald 1992, Land 2005, Zurek et al. 2010). However, the visual system in salticids is unusual mainly due to its principal eyes (anterior medial eyes, AME); these have an exceptional spatial acuity vastly exceeding any other animal with a similar eye size (Williams & McIntyre 1980, Land 1981, 1985, Harland et al. 1999, Schwab & Jackson 2006).

The AME are an example of convergent evolution of camera-type eyes, which are also found in vertebrates and cephalopods (Nilsson 2013). Briefly, the AME consist of the cornea, the lens, a long eye tube, and a boomerang-shape retina lying at the end of the eye-tube (Land 1969a). The retina comprises four layers of photoreceptors that have colour discrimination ability (Harland et al. 2012) and may enable depth perception (a mechanism named as image-defocus, Nagata et al. 2012). The retina can be moved laterally up to 35º to either side of the body axis, as well as vertically, and they can rotate on-axis (Land 1969b) in order to track a specific object in high resolution.

Spatial acuity refers to an eye's visual angle ("the minimum separation required before objects in a scene are seen as separate", Harland et al. 2012), such that the smaller the visual angle, the higher the resolution. The smallest visual angle in insects is found in dragonflies (0.4º, Labhart & Nilsson 1995), and the visual angle of the human eye is 0.07° (Kirschfeld, 1976). The visual angle of the salticid AME is 0.13° in a typical salticid (Land 1969a, Blest et al. 1988), or up to 0.04º in *Portia fimbriata* (Williams & McIntyre, 1980). This is exceptional, as an entire salticid body can be smaller than the dragonfly's eye, but its eyes still have at least three times better spatial acuity. However, the AME have a narrow field of view of 3-5º (Land 1969a,b, Williams & McIntyre 1980, Blest et al. 1990), although they can move the retinae internally.

Salticid vision is highly complex not only because of the AME but also because of the interaction between the AME and the secondary eyes. The latter are known to have a motion-detection function, informing the spider about moving objects in their visual field and initiating

optomotor responses to face the movement object in order to further identify it with the AME. Yet more interesting is the possible function of the pair of anterior lateral eyes (ALE) in depth perception. The two ALE have widely overlapping visual fields, which, it is speculated, may be used for binocular depth perception (Harland et al. 2012).

Information about visual perception has been discovered by use of both morphological and behavioural studies, but a clear understanding of visual perception in salticids is far from being achieved. For example, despite some inferences about depth perception as a result of meticulous molecular and electrophysiological work, behavioural tests gave rather inconclusive evidence of the use of image defocus as the absolute depth perception mechanism in salticids (Nagata et al. 2012). However, in animals, behavioural experiments with visual illusions have proven to be useful, not just in terms of visual perception, but also to understand cognitive and neuropsychological mechanisms of image processing as a whole (Kelley & Kelley 2014). Visual illusions can be defined as effects that distort the perception of the viewer towards an object's visual properties (size, distance, shape, coloration or movement). Unlike simple images, visual illusions show abstract representations that may or may not be formed in the receiver's brain. Therefore, these are useful tools for comparative studies between different species - and different optical systems (Kelley & Kelley 2014).

Visual illusion experiments often require training and are relatively tractable in vertebrates because tasks can be incorporated as preference tasks as a consequence of associations with food (e.g., pecking in birds). However, in invertebrates the number of species that can be easily trained is reduced, and visual illusions need to be tested in the context of biological importance for the species in order to work (Neumeyer 1980, van Hateren et al. 1990, Kinoshita et al. 2012), although the same is also true of other vertebrates. Nevertheless, studies show that visual illusions are not always perceived the same way, even when the subjects have the same eye structure (e.g., humans and pigeons, Nakamura et al. 2008, Watanabe et al. 2011); yet sometimes the visual illusion works across species with very different eye types (e.g., camera-type eyes in humans and compound eyes in bees and butterflies: Neumeyer 1980, van Hateren et al. 1990, Kinoshita et al. 2012; humans and cuttlefish: Zylinski et al. 2012, Josef et al. 2014).

A potential approach to understand visual perception, and specifically depth perception in salticids, could be the use of visual illusions in the context of risk assessment. As recently demonstrated (Josef et al. 2014), cuttlefish react aversely to depths, which allowed to scientists to use an optical illusion of a representation of a trench to explore responses to illusions. Innate aversion to depths, or 'drops', are widely represented in animals (e.g., rats: Nealey & Edwards 1960; chickens: Shinkman 1963; pigs, lambs, dogs, cats, turtles: Walk & Gibson 1961; cuttlefish,

Josef et al. 2014), and possibly among salticids which often are faced with jumping across branches or leaves at considerable height. Certain elements, such as the texture density gradient (a graded change in the size of the elements on a surface) can be manipulated in such a way that a 2-dimensional image can be perceived as a 3-dimensional surface (Gibson et al. 1955, Frisby & Stone 2010), as demonstrated by the 'trench' illusion used by Josef et al. (2014), which resembles a trench that sinks in a 2-dimensional checkerboard pattern.

In **Chapter 5**, we endeavour to further understand salticid depth perception, which is still poorly understood, under the context of textural information. Firstly, we explored depth perception while exposing spiders to the 'trench' illusion, hypothesising that spiders would be fooled by it behaving aversely towards this visual pattern compared to a control pattern. We then performed a 'visual cliff' experiment and a modified version of the visual cliff experiment to test whether spiders are height-averse and whether they use texture density as a cue to perceive depth. Our hypotheses were that spiders would avoid the high drop area and the area with lower texture density, respectively. Finally, we controlled for binocular and monocular depth perception mechanisms in a test to determine the mechanism used by spiders in order to: a) accurately assess the distance to perform a targeted jump, and b) assess the risk of jumping over a gap with different heights. The hypothesis was that spiders would perform similarly with and without binocular cues provided by the ALE, as it is possible that salticids may rely on a monocular depth perception mechanism (e.g., Nagata et al. 2012).

Final note

I collected and analysed all data, but initially had help from a statistician (Dr Daniel Gerhard). Along with my supervisor, Ximena Nelson (and for **Chapters 4** and **5** from Dr Alex Taylor from the University of Auckland), I conceptualised the experiments and wrote over 85% of the information contained in this document. As no scientific endeavour is done single-handedly, throughout this document I refer to myself in the first-person plural (i.e., we/our).

Finally, **Chapter 2** has been published as: Aguilar-Arguello S, Gerhard D, Nelson XJ 2020. Distance assessment of detours by jumping spiders. *Current Zoology 66, 263-273.* doi:10.1093/cz/zoz044, and **Chapter 3** has been published as: Aguilar-Arguello S, Gerhard D, Nelson XJ 2019. Risk assessment and the use of novel shortcuts in spatial detouring tasks in jumping spiders. *Behavioral Ecology 30,* 1488-1498. doi:10.1093/beheco/arz105. The remaining two chapters are being prepared for publication.

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CHAPTER TWO. Distance assessment of detours by jumping spiders

Birdling's flat, the natural environment in which *Marpissa marina* lives.

Abstract

To take an indirect route (detour) in order to reach a specific target requires complex cognitive processes. Yet more demanding, from the cognitive point of view, is when the goal is only visible at the beginning of the detour. In spiders from the family Salticidae, vision is a key sensory modality mediating navigation and prey search. Their acute vision allows them to perform complicated detours, possibly as a consequence of the multitude of potential routes in their typically complex three-dimensional habitats. We used a four-route choice test, in which routes differed in being either short or long and in the presence or absence of a lure of a prey item, to investigate route assessment in two salticid species, *Trite planiceps* and *Marpissa marina*. Although both species showed evidence of motivation to follow lured routes, judging by the number of times they re-oriented towards them while detouring, we found that *Trite* chose short routes in preference to long routes, but did not prefer the lured-routes. In contrast, *Marpissa* exhibited random route choice, although it oriented toward lured-routes more often than control routes (lure absent). Our results suggest that decision-making processes about which route to take occurs before embarking on a route, but this is cognitively challenging. Spiders exhibited cognitive limitations in which the lack of visibility of the goal affected success. However, the severity of cognitive limitations depended on species. We suggest that variability in spatial ability across the Salticidae may be related to the habitat complexity inhabited by each species.

Introduction

The cognitively simple process of moving in a straight line towards a visualised goal occurs as an instinctive response (Köhler 1927). However, using an indirect route to reach a goal (detouring), requires mental operations beyond innate responses, such as different types of learning, and disruption/retention mechanisms (Kabadayi et al. 2018). Even more complexity is required when the goal becomes invisible while the individual executes the detour. In this case, without the use of cues emanating from the goal, the subjects rely on working memory, route planning, and orientation (Wells 1967, Cross & Jackson 2016). The latter detours can be performed by vertebrates (Regolin et al. 1995, Zucca et al. 2005), and also by invertebrates with outstanding eyesight, such as octopuses (Wells 1970) and jumping spiders (Araneae: Salticidae) (Cross & Jackson 2016). Salticids are characterised by their highly acute vision (Land 1969, Harland et al. 2011) based on a visual system comprised of one pair of principal eyes and three pairs of secondary eyes. The principal, or anterior medial eyes (AME), are crucial for high spatial acuity and colour

vision, whereas the secondary eyes can detect motion over about 360° surrounding the spider (Harland et al. 2011).

In salticids, vision is a key sensory modality mediating prey capture (Jackson 2000, Li et al. 2003), agonistic displays (Wells 1988, Taylor et al. 2001), visual courtship (Clark & Morjan 2001), and navigation (Hoefler & Jakob 2006). When foraging, salticids visually identify their prey at a distance (Richman & Jackson 1992) and stalk prey using a readily observable set of behaviours: the spider initially orients its cephalothorax towards the prey with the AME facing it - a behaviour known as 'orientation', after which, if prey is identified, the salticid slowly approaches and finally catches it by pouncing from 2-3 cm (Forster 1977). When a direct route to reach a visually-located prey is not available, salticids may perform detours (Punzo 2004; Jakob et al. 2011). Detouring implies route planning (Cheng 2016) and spatial learning or ability (Thorpe 1963; Healy 1995). Scanning behaviour, in which salticids systematically move their cephalothorax and body to inspect their surroundings using their AME, precedes detours, and is believed to be crucial for *a priori*-based route selection (Tarsitano & Andrew 1999, Cross & Jackson 2016). However, while detouring, salticids may not always see the goal, and may rely on spatial memory or on an internal representation of the prey's relative position (Hill 1979, Tarsitano & Jackson 1992, Tarsitano & Andrew 1999, Tarsitano 2006). During a detour, salticids often 're-orient' towards the location of the goal in order to keep track of it (Hill 1979). Such re-orientations allow the spider to readjust its detour or stop detouring if the goal (e.g., prey) moves to another location. Detours are represented by a sub-goal (e.g., leaf or branch), or a series of sub-goals, that spiders need to initially reach to enable access to the main goal. Hence, using detours implies making associations of sub-goals that will lead to the primary objective. Hill (2007) suggested that salticids can use tertiary and possibly quaternary objectives depending on the length and complexity of the detour.

Commonly living in complex three-dimensional environments, salticids are likely to encounter several possible detours that may or may not lead to a desired goal. Thus, decision-making becomes essential from an adaptive point of view (Punzo 2000), as choosing the most efficient route (the one that leads to prey, the shortest, the safest, etc.) allows the spider to save time and energy, and to be less vulnerable to predators (Gibson et al. 2007). Several salticid species have been shown to take detours (Hill 1979, Tarsitano & Jackson 1992, 1994, Carducci & Jakob 2000; Cross & Jackson 2016), suggesting this to be a common behaviour in this family. Previous studies about detour assessment in salticids have focused on testing spatial abilities of species in the subfamily Spartaeinae (Jackson & Wilcox 1993, Tarsitano & Jackson 1994), and the majority of these studies provide two alternate detours (one detour leading to prey and a no-prey control; Tarsitano & Jackson 1992, 1997, Tarsitano 2006, Cross & Jackson 2016). However, detour

assessment combining length and the presence of prey as factors has not yet been tested. We tested this using a four-choice test with two long and two short routes, with a prey lure on one of the long and on one of the short routes. Using two species of salticids from the Salticoida subgroup, *Marpissa marina* Goyen and *Trite planiceps* Simon, we wanted to determine: 1) if salticids are able to decide on a route during the scanning phase before embarking on a route, and remember this even after the goal is visually blocked; 2) if salticids prefer short routes over long routes; 3) if there are species-specific differences in spatial ability.

As salticids can follow a secondary objective while apparently memorising the spatial location of the goal (Hill 1979), we predicted that the spiders would reach the goal even if they could only see it at the beginning of the task. We also expected that salticids would choose the short route leading to prey compared with the other three routes; this being the most efficient route to a goal. It is known that closely related species can differ in spatial ability as a consequence of the environment in which they live (Kasumovic 2013) because the environment can directly affect cognitive (van Praag et al. 2000) and spatial abilities (Parker & Gibson 1977, Striedter 2005, Park & Bell 2010). Consequently, we expected *Trite* to outperform *Marpissa*, because it inhabits a three-dimensionally more complex habitat.

Methods

Test animals

All animals were collected in Canterbury, New Zealand. Experiments were carried out from 0800 to 1300 h in the laboratory at the University of Canterbury. *Trite planiceps* is a large (6-13 mm) salticid endemic to New Zealand and is typically found in coastal areas where it inhabits the rolled-up flax leaves of *Phormium tenax* and *Cordyline* spp. (Forster 1979). *Trite* were field-collected in Christchurch and were transferred to the laboratory, where they were housed individually in 1-litre transparent plastic containers. Individuals were held in captivity for at least one week before testing. Water supply was available through a cotton wick submerged in water which protruded into the container. Spiders were fed weekly with two adult *Musca domestica*. Hunger level during testing was standardised by performing the tests 5-7 days after their previous meal, thus ensuring similar hunger levels between individuals.

Marpissa marina is native to the South Island of New Zealand. It lives in quite flat rocky shores and makes nests 2-6 m above the high tide mark (Vink & McQuillan 2015). Adult males are 5-8 mm and females 6-9 mm in body length, and subadults are typically about 1 mm smaller than adults. Collected individuals were housed and maintained as described for *Trite*.

Experimental setup

We exposed spiders to four different routes from which to choose in order to reach a prey (i.e., lure made from a dead fly on the goal platform, described below). To determine if spiders were able to evaluate, or cared about, the distance of the route to reach a prey, the routes were either long or short. Additionally, to identify if spiders were actually following a route because of the prey rather than as a consequence of random choice, the goal platforms at the end of each route either did, or did not, have prey. Thus, the four different routes were: 1) short-lured route; 2) long-lured route; 3) short-control route; 4) long-control route. We tested 53 *Trite* (23 females, 16 males, and 14 subadults) and 63 *Marpissa* (25 females, 19 males, and 19 subadults).

The arena (see **Figure 1** for dimensions) consisted of an aluminium tray with a central starting platform (a wooden dowel) on which the spider was placed at the beginning of every trial. Surrounding the starting platform there were four routes made of articulated plastic sections (each 2.5 cm long) with magnetic bases. Short routes had 10 articulated sections (25 cm) and the long routes had 22 sections (55 cm). The distance from the starting platform to the goal platform on a long route was 114 cm, and 84 cm for short routes. All goal platforms were at the same height (20 cm) and distance (17 cm) from the starting platform, with the route bases being 30 cm from the base of the starting platform. Consequently, the spider could see the four goal platforms at the same distance and height from the starting platform. External visual cues were blocked by black screens and the corner wall of the laboratory.

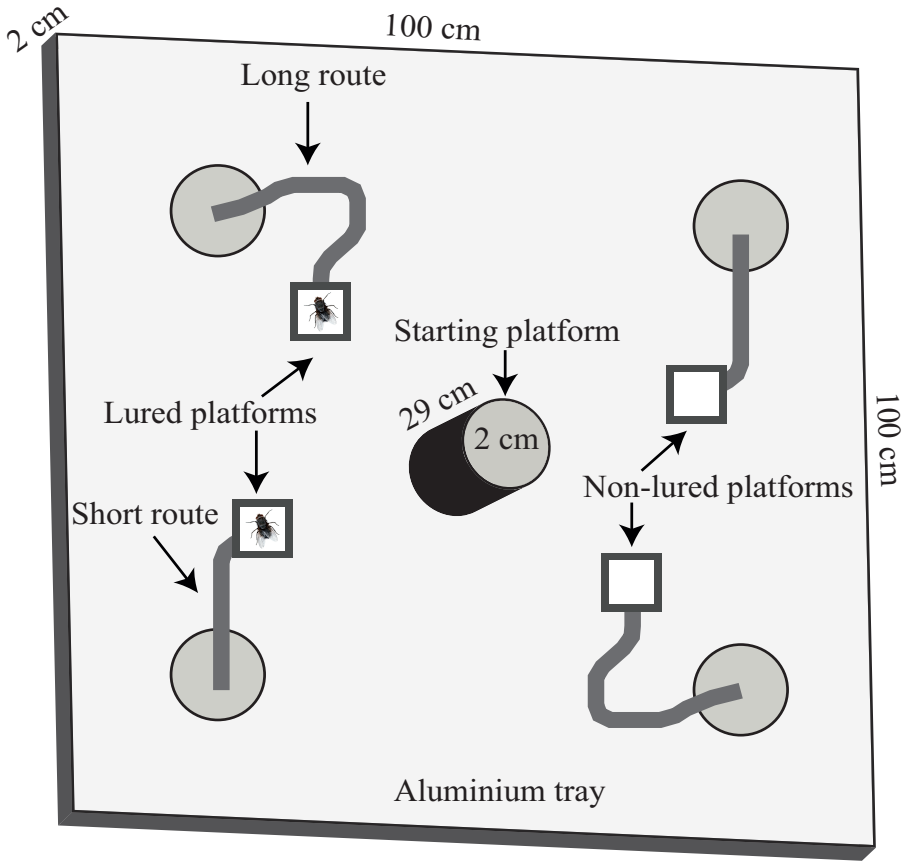

Figure 1. Aerial view of experimental arena (not to scale). To begin a test, spiders were placed on the starting platform from which they observed the four different routes to goal platforms with or without dead prey (lures).

Goal platforms consisted of a square plate (4 x 4 cm) of aluminium with an attached 'jiggler'. The jiggler allowed 5 Hz movement of a rigid wire (15° to each side of the vertical for 2 s; Dolev & Nelson 2016) to simulate prey movement when a lure was stuck on the wire. In control route goal platforms, this was comprised by the wire and a thin (1 mm) disc of cork, while in prey goal platforms, a dead prey on a thin cork disc was attached to the wire. Lures were adults of *Musca domestica* attached to the cork disc in a lifelike position and covered with transparent aerosol plastic adhesive (Jackson & Cross 2015). Jiggler movement, which serves to maintain the spider's attention, was activated only when the spider was facing a goal platform and any movement was stopped when the spider left the starting platform.

Spiders were placed on the starting platform in the centre of the arena to begin a test. This allowed them to visually scan their surroundings to identify a goal, as once the spiders left the starting platform toward the base of the arena, visual cues on the goal platforms were no longer

visible to test spiders. To eliminate directional bias, we randomly rotated the arena in one of four locations (North, South, East, and West). The position of the lures with respect to the routes (lure configuration) was also randomised for every trial. Consequently, each spider was exposed to one cardinal location plus one lure configuration. Each trial lasted 20 mins, or less if the spider reached the lure; exceptions occurred when 20 mins elapsed but the spider had started climbing one route. In these cases, trials ran until the salticid reached the end of the route or until it jumped off the route. However, if 20 mins had elapsed and spiders had not left the starting platform or if the spider reached the edge of the arena, the spider was re-tested the next day. The arena was wiped with 80% ethanol between tests.

Analyses

Each trial was recorded with a Logitech c920 HD Pro webcam (1080 pixels at 30 fps) placed 40 cm above the arena. In our analyses we accounted for spider species and age/sex category (adult male, adult female, subadult). From our footage we scored 'initial heading', defined as the final orientation towards any of the four goal platforms just before approach (either by walking or jumping toward it), suggesting initial route preference (Tarsitano 2006). As the initial heading did not always coincide with the final chosen route, these data were qualified with 'decided' if the initial heading coincided with the chosen route, or 'undecided' if it changed. When spiders did not exhibit an initial heading, this was scored as N/A. We also scored the frequency of orientations during the scanning phase (i.e., a turn of the cephalothorax towards the goal platform while the spider was at the starting platform). The number of re-orientations during the detour were also recorded (see **APPENDIX 1.1**). Additionally, we measured 'scanning duration' as the elapsed time from when the spider started scanning until it left the starting platform, as well as the time from the end of scanning phase to the end of the trial ('route duration'), the chosen route, the cardinal 'direction' of the chosen route, and the position within the route at which the spider abandoned the route, or 'giving up point' (Tarsitano & Jackson 1997). This was divided into four sections: 1. passing the magnetic base of the chosen route base but advancing no further; 2. climbing no more than half-way up the route; 3. reaching the second half of the route; 4. reaching the goal platform or the last plastic articulation of the route (2.5 cm before the platform).

All analyses were done using R v.3.3.3 (R Development Core Team, 2018). To determine route preferences, we performed two comparisons of multinomial probabilities for count data for each species. We calculated simultaneous confidence intervals for the comparison of multiple odds between multiple multinomial samples (following Schaarschmidt et al. 2017) using the 'multcomp' (Hothorn et al. 2008) and 'nnet' (Venables & Ripley 2002) packages. We excluded highly influential

data (outliers) from the model with a Cook's distance value (which combines the leverage and residuals of each data point) > 0.5 (Crawley 2007). The first analysis compared the probability of choosing a specific route (the route with the highest probability to be chosen) with the probability to choose the other three routes separately. Here, the baseline was the route with the highest probability of being chosen (short-lured route for *Trite*; long-lured for *Marpissa*). The second analysis compared the probabilities to choose either long or short routes, and either control or lured routes, plus their interactions (see Schaarschmidt et al. 2017).

To identify if spiders followed a specific route as a consequence of decision-making while on the starting platform and not by choices made after leaving the platform, we analysed the final choice with respect to the initial heading for each species. Data from spiders that did not orient to any route before leaving the starting platform (N/A) were omitted. Here, we used a comparison of multinomial probabilities (for count data) to determine if the probability of a route being chosen depended on its congruence with the initial heading (i.e., 'decided' spiders). Here we used 95% confidence intervals (CI), calculated using both Dirichlet (DP) and Wald methods. In these cases, a P value < 0.05 is found when "1" is contained within the CI for the odds ratio between decided and undecided spiders, such that the hypothesis that the groups are not different is rejected (Schaarschmidt et al. 2017).

Initial choice may not concur with the chosen route because spiders may not choose based on the last orientation toward a route before leaving the starting platform, but instead may survey the possible alternatives during the entire scanning phase. Consequently, the number of orientations during the scanning phase may be a better indicator of an association between the targeted route at the starting platform, and the chosen route at the end. In this case, we predicted that spiders that associate the correct route to their final goal (which we expected to be lured-routes, especially short ones) would have a higher number of orientations during scanning. To determine if this, we performed a GLM with a Poisson distribution with the number of orientations as the response variable. Spider category and chosen route were used as explanatory variables in the model for *Trite*, all of which completed routes. For *Marpissa*, we omitted three outliers (values: 14, 16, and 20 orientations). This model accounted for spider category, chosen route, and giving up point as explanatory variables, as several *Marpissa* did not complete routes. Contrast tests were then applied with the 'gmodels' package (Warnes et al. 2015). Additionally, to determine whether the completion of the route (as a binary variable) depended on the number of goal orientations in *Marpissa*, we analysed the data with a binary logistic regression, with completion of the route (0 = incomplete routes, 1 = completed routes) as the response variable and the

number of goal orientations as the independent variable (Crawley 2007); we omitted one outlier for this analysis.

To investigate species-specific differences, we used the general dataset (this includes trials in which the individual chose a route irrespective of whether it was completed). Here, we performed a comparison of multinomial probabilities for count data, using the four routes as the categories (chosen route) and species as the treatment groups. The first analysis compared the baseline (short-lured) route with the other three routes. The second analysis was a specific comparison using the Wald and DP methods. The latter compared the probability to choose either control routes and lured routes, or short routes and long routes. To determine whether the number of orientations differed between species, we performed a GLM with a Poisson distribution, omitting N/A's and excluding outliers from three *Marpissa* individuals. Orientations were the response variable and species the explanatory variable. We used the same analysis, using data from completed routes only, to explore differences in the number of re-orientations (see **APPENDIX 1.1**).

We analysed scanning duration and route duration using accelerated Failure Time Regression (AFT) survival models, allowing us to compare the hazard function, or the risk of an event to finish, and a set of explanatory variables. Each AFT model was selected based on the distribution with the minimum AIC value, which exhibited the best fit to the data (Cox 1972). Second-order interactions among the explanatory variables were not accounted for, as the AIC value for the full model was higher than the selected model. Scanning duration was set as the response variable, with species, chosen route, and spider category as explanatory variables. With this configuration, we ran two AFT models using different datasets: the first model (Weibull distribution) used the general dataset, while the second used the subset of spiders that completed a route ('giving up point' = 4); in this model a loglogistic distribution was selected to better fit the data.

For route duration, the selected AFT model accounted for route duration as the response variable and species, spider category, and chosen route as the explanatory variables. Based on the AIC value, the best-fit error distribution for the general dataset was loglogistic. Additionally, we ran survival analyses using individuals that completed the route only; therefore, all 53 *Trite* individuals were included in the model, but only 25 *Marpissa*. Model selection was performed under the step model and here the best-fit error distribution was lognormal.

Results

For those spiders that made a choice, the log-odds between decided and undecided spiders did not differ between routes, either for *Trite* or *Marpissa* (**Figure 2**; **Table 1**; **Table 1** in **APPENDIX 1** for probabilities). Additionally, when comparing control and lured-route choices, we found no difference in odds-ratio between decided and undecided *Trite* (95% CI for odds-ratio: DP method: lower = 0.35, upper = 12.01, Wald method: lower = 0.29, upper = 15.95) or *Marpissa* (95% CI for odds-ratio: DP method: 0.80, 15.16, Wald method: 0.75, 20.51), nor were there differences between long and short routes (*Trite*: DP method: 0.17, 5.47, Wald method: 0.13, 6.98; *Marpissa*: DP method: 0.10, 1.86, Wald method: 0.07, 1.99).

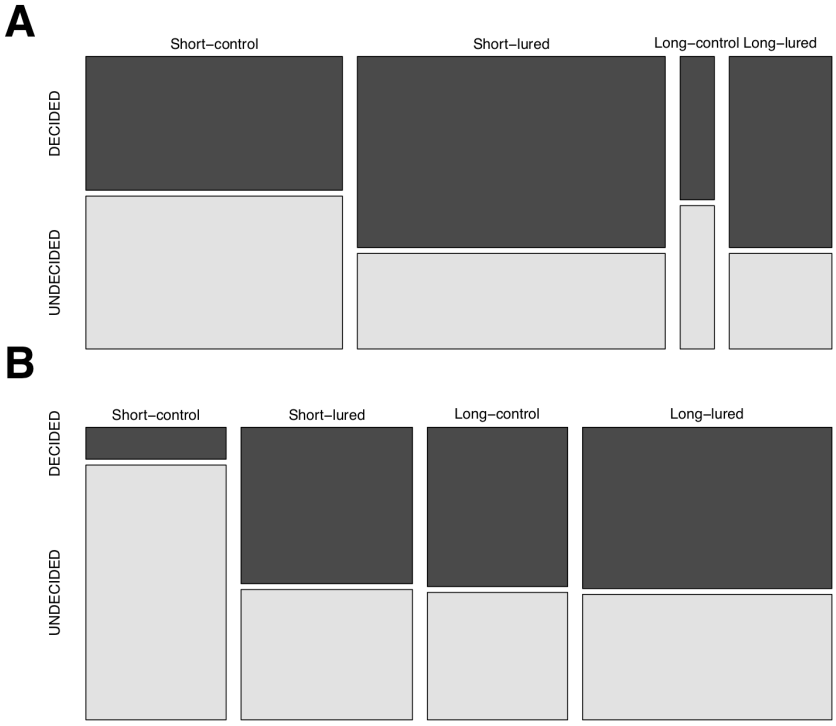

Figure 2. Mosaicplot showing the proportions of (**A**) *Trite* and (**B**) *Marpissa* individuals that did not change (decided) and those that changed their choice (undecided) for the four routes.

Table 1. Comparison of multinomial probabilities for number of decided/undecided spiders between the short control route and the other three routes chosen by *Trite* and *Marpissa*.

Trite				
Comparisons between route variables (decided/undecided)	Estimate (odd-ratio)	SEM	*Z*	*P*
Short-lured/Short-control	0.826	0.719	-1.149	0.561
Long-control/Short-control	0.135	1.506	-0.089	1
Long-lured/Short-control	0.826	1.008	-0.89	0.783
Marpissa				
Short-lured/Short-control	2.262	1.221	-1.852	0.129
Long-control/Short-control	1.856	1.255	-1.479	0.26
Long-lured/Short-control	2.33	1.174	-1.985	0.097

The number of orientations toward the chosen route was higher (estimate = 0.4908, Z = 4.186, $P < 0.0001$) in *Trite* (mean ± SEM; 3.32 ± 0.45) than *Marpissa* (2.03 ± 0.32). *Trite* which chose the short-control route made significantly less orientations (**Figure 3A**) compared with the other three routes, and subadults oriented more than females and males (**Figure 3B**; **Table 2** in **APPENDIX 1**). In contrast, in *Marpissa*, the number of orientations was not influenced by chosen route or spider category, but was significantly higher among spiders that completed all four sections of the route, rather than those that gave up early (**Figure 3C**; **Table 3** in **APPENDIX 1**; note that no *Trite* gave up early). This was confirmed using a binary logistic regression which showed that *Marpissa*'s probability to complete routes was related to the number of goal orientations (95% CI = 0.029 to 0.509, estimate = 0.2699, Z = 2.203, P = 0.027; **Figure 1** in **APPENDIX 1**). Similar trends were found with the number of re-orientations (**Figures 2**, **3** and **Tables 4**, **5** in **APPENDIX 1**).

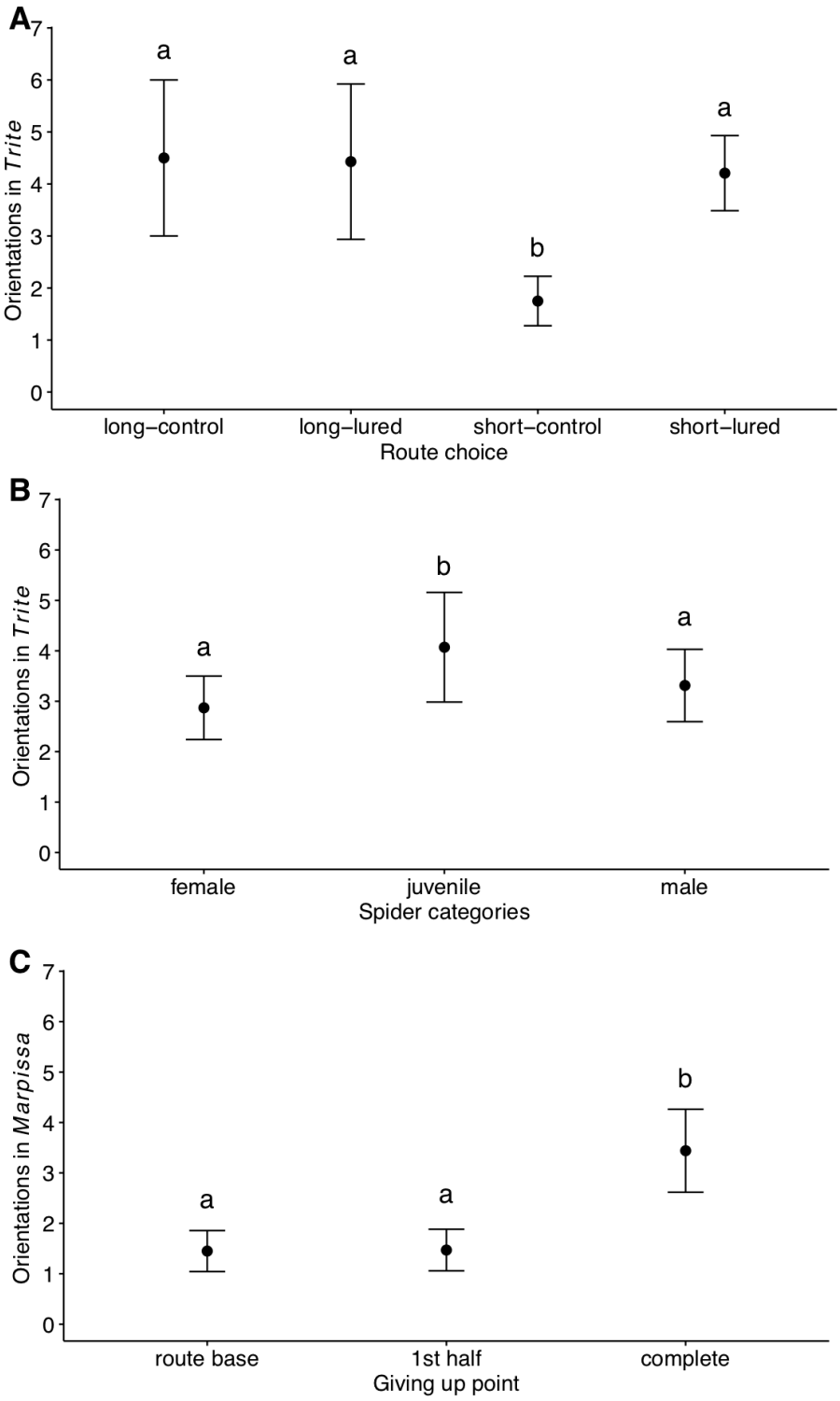

Figure 3. Mean (±SEM) number of orientations by (**A**) chosen route in *Trite*, (**B**) *Trite* spider category, (**C**) giving up point in *Marpissa*. Letters indicate significant differences between groups.

In *Trite*, the probability to choose lured, compared to control, routes did not differ and there was no interaction between lure presence and route length (**Table 2**). Although the probability to choose the short-lured and short-control routes did not differ, *Trite* was more likely to choose short routes (**Figure 4**). In *Marpissa*, there were no differences in the probabilities to choose any route, nor were there any interactions, both among spiders that completed routes, and all spiders from the general dataset (**Table 2**). When comparing the general dataset for both species, the log-odds between choosing long-control with respect to short-lured routes and choosing long-lured compared with short-lured routes were significantly higher in *Marpissa* than *Trite* (**Table 3**). However, the odds ratio of choosing short-control with respect to short-lured routes did not differ between species (**Figure 5**). The odds ratio of choosing long routes with respect to short routes was significantly higher in *Marpissa* (95% CI for odds-ratio: DP method: lower = 2.05, upper = 15.98, Wald method: lower = 2.04, upper = 18.82). However, the odds ratio between control and lured routes did not differ between species (95% CI for odds-ratio: DP method: lower = 0.53, upper = 15.98, Wald method: lower = 0.51, upper = 4.70).

Across all spiders, the probability to remain at the starting platform scanning the surroundings (scanning duration) was not significantly affected by the chosen route (**Table 6** in **APPENDIX 1**). Nevertheless, there were species-specific behavioural differences, with *Marpissa* scanning for longer than *Trite* (max: *Trite* 966 s, *Marpissa* 1934 s; P_1 = 0.016; **Figure 6A**). Additionally, females scanned for longer than subadults (**Figure 6B**). The same effects were found when considering only individuals that completed a route (**Figure 6C**, **D**). The time to reach the giving up point was also unaffected by species, spider category, or by chosen route. However, route duration was lower in males than females, both for all spiders (**Figure 7A**; **Table 7** in **APPENDIX 1**) and among spiders that completed a route (**Figure 7B**). In the latter subset, *Trite* was faster than *Marpissa,* **Figure 7C**) and spiders that chose long routes took longer than those choosing short routes (**Figure 7D**; **Table 8** in **APPENDIX 1**).

Table 2. Results from the comparisons of the probability to choose the short-lured route in *Trite* and *Marpissa* with the other three routes, as well as comparison between the probabilities to choose the routes by its length and/or presence of lure. Data for *Marpissa* includes those from all individuals that chose a route (general dataset) and from completed routes dataset.

Trite*				
Comparisons between routes	Log-odds	SEM	Z	*P*
Long-lured/Short-lured	-1.232	0.429	-2.868	0.012
Long-control/Short-lured	-2.489	0.736	-3.376	0.002
Short-control/Short-lured	-0.182	0.302	-0.602	0.901
Comparisons between route variables				
Control-routes/Lured-routes	-0.717	0.428	-1.674	0.210
Short-routes/Long-routes	1.767	0.428	4.124	0.0001
Interaction†	-0.535	0.428	-1.249	0.429
General dataset (Marpissa)*				
Comparisons between routes	Log-odds	SEM	Z	P
Long-control/Long-lured	-0.559	0.361	-1.546	0.297
Short-lured/Long-lured	-0.336	0.338	-0.995	0.649
Short-control/Long-lured	-0.336	0.338	-0.995	0.649
Comparisons between route variables				
Control routes/Lured routes	-0.279	0.257	-1.089	0.618
Short routes/Long routes	-0.056	0.257	-0.22	0.995
Interaction†	-0.279	0.257	-1.089	0.618
Dataset for completed routes (Marpissa)**				
Comparisons between routes				
Long-control/Long-lured	-0.559	0.626	-0.893	0.71
Short-lured/Long-lured	-5.13e-06	0.534	0	1
Short-control/Long-lured	-5.13e-06	0.534	0	1
Comparisons between route variables				
Control routes/Lured routes	-9.225	47.510	-0.194	0.860
Short routes/Long routes	-8.127	47.510	-0.171	0.878
Interaction†	-8.820	47.508	-0.186	0.867

P values by route: *Long-lured (n = 7, *P* = 0.132), Long-control (n=2, *P* = 0.037), Short-lured (n = 24, *P* = 0.452), Short-control (n = 20, *P* = 0.377). **Long-lured (n = 21, *P* = 0.333), Long-control (n = 12, *P* = 0.190), Short-lured (n = 15, *P* = 0.238), Short-control (n = 15, *P* = 0.238). ***Long-lured (n = 7, *P* = 0.28), Long-control (n = 4, *P* = 0.16), Short-lured (n = 7, *P* = 0.28), Short-control (n = 7, *P* = 0.28). †model accounts for the interaction between route length and lure incidence.

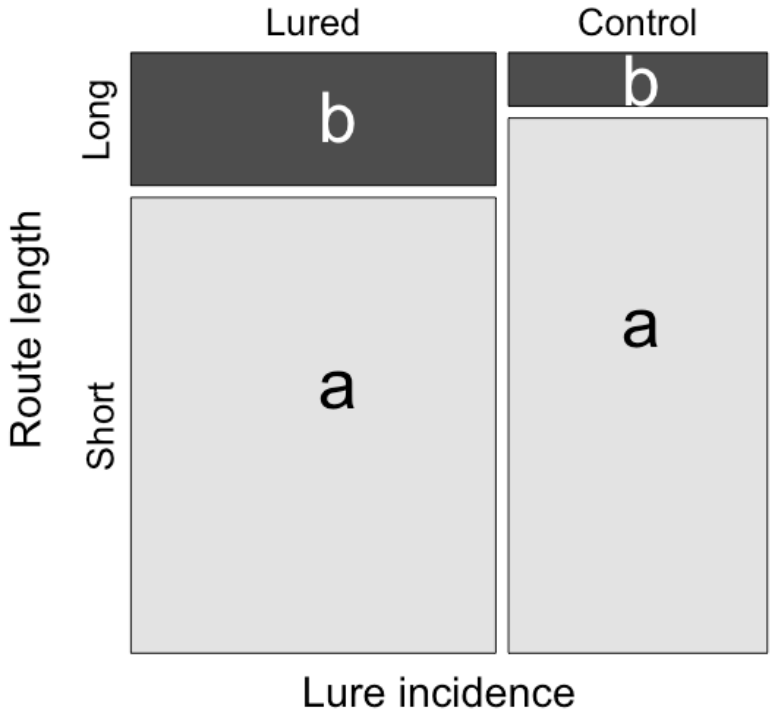

Figure 4. Mosaicplot of the frequency of choices in *Trite planiceps* on the four different routes.

Table 3. Results from the multinomial comparison of the number of individuals of each spider species that chose each route.

Comparisons between routes (*Marpissa*/*Trite*)	Log-odds	SEM	*Z*	*P*
Long control/Short-lured	-2.261	0.837	-2.720	0.019
Long-lured/Short-lured	-1.568	0.546	-2.870	0.012
Short control/Short-lured	-0.182	0.474	-0.384	0.969

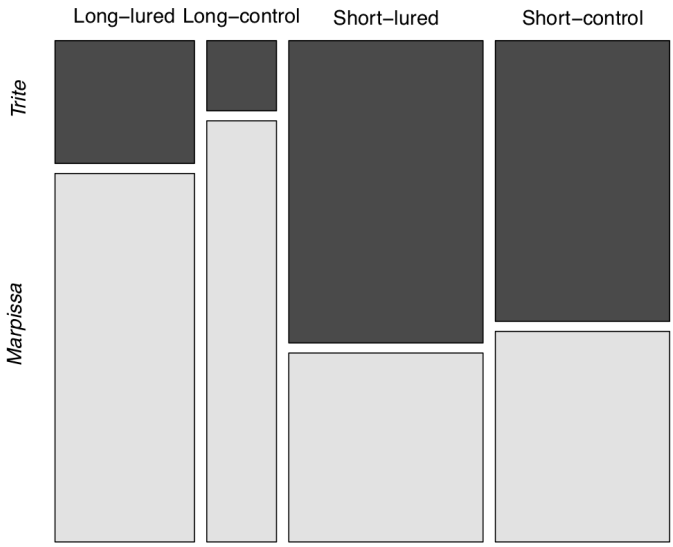

Figure 5. Mosaicplot of proportion of choices for each route in both spider species.

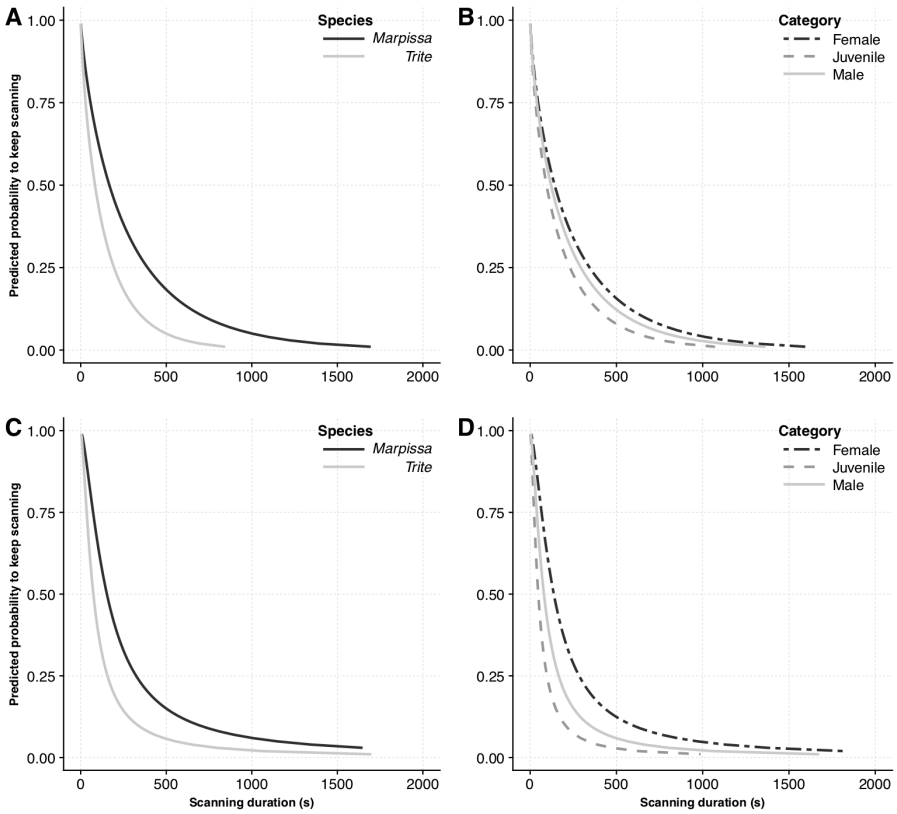

Figure 6. Accelerated Failure Time model curves depicting the probability of continuing scanning over time for (**A**) all *Marpissa* and *Trite*, (**B**) spider categories of both species combined, (**C**) data from completed routes only for *Marpissa* (2 values with duration > 2000 s not shown)

and *Trite* (1 value with duration > 2000 s not shown), (**D**) spider categories (1 female value with duration > 2000 s not shown, completed routes only).

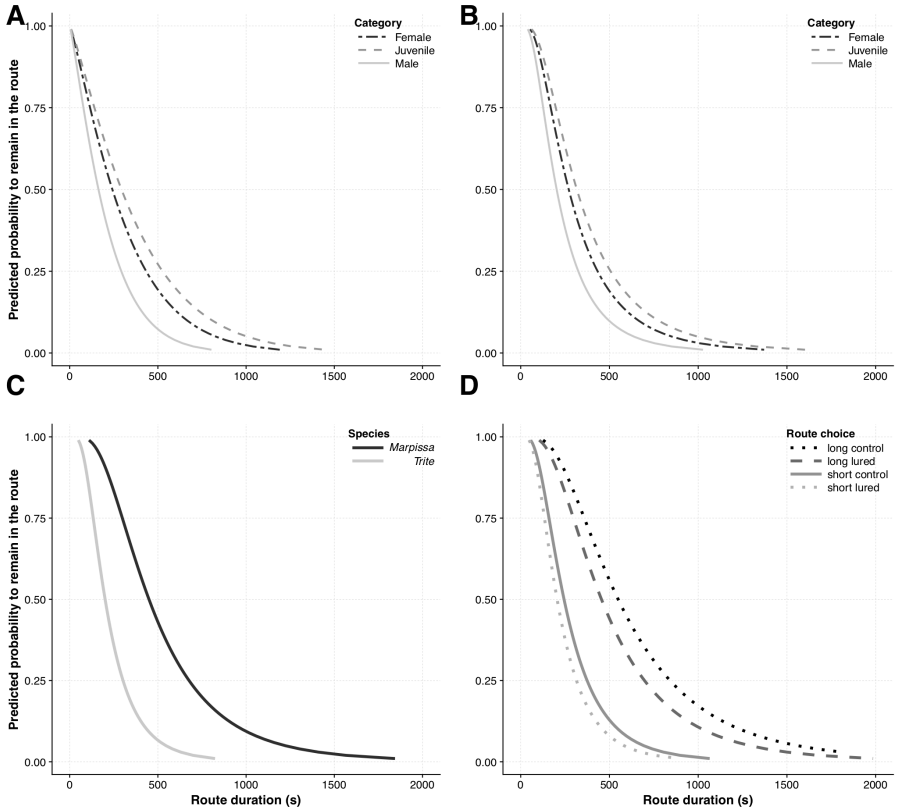

Figure 7. Accelerated Failure Time model curves depicting the probability of continuing on the chosen route over time for each spider category spiders for (**A**) all spiders, irrespective of whether routes were completed; and (**B**) spiders that completed routes only. (**C**) species difference s between *Marpissa* and *Trite* that completed routes, (**D**) route category for spiders that completed routes (data not shown for two individuals choosing long-control route as these lasted > 2000 s). Note: panels have different X-axis scales.

Discussion

This study provides evidence of cognitive limitations while performing spatial tasks in two salticid species, contributing to a broader view of the differences of spatial ability within the Salticidae. In comparison with previous studies, our detouring tasks were especially complex (four choices varying in length and presence of prey and in which visual access to prey was denied after leaving the starting platform). Nevertheless, we found evidence that spiders are able to make decisions while on the starting platform before embarking on a route, and we also observed interspecific differences in route-choice behaviour. While we anticipated that the short-lured route would be preferred, due to being more efficient (shorter) and containing prey, spiders did not exhibit this preference. *Trite* did prefer short over long routes, but showed no preference for lured routes, possibly because the task was too cognitively demanding. In *Marpissa*, spiders showed no route preference, and may have chosen routes randomly. However, arguing against this, in their frequency of orientations and re-orientations, *Marpissa* demonstrated some evidence that they can discriminate lured from control routes.

Route choice did not affect scanning or route duration for either species, but *Trite* completed routes faster than *Marpissa*, which may have struggled more to solve the task than *Trite*: although *Marpissa* spent more time scanning, the number of orientations was lower than *Trite*'s, and *Marpissa* only completed routes when they frequently oriented (and re-oriented) towards the goal platform. Indeed, compared with the salticid *Portia*, *Trite*'s fast performance in spatial tasks previously suggested to us that *Trite* faces a trade-off between fast route completion but deficient route assessment (Aguilar-Arguello et al. 2019). We cannot discard that previous experience with houseflies in nature may have caused different behaviours between species, as we have little information about housefly availability in their natural habitats, other than they exist in both habitats. However, for decades houseflies have been used as standard prey for predator-related experiments for both of these species (e.g., Forster 1977, 1979, Tarsitano & Jackson 1992, Jackson & Tarsitano 1993), confirming that houseflies are attractive prey. We also found that spider categories behaved similarly across species, with subadults finishing the scanning phase faster. As it is known that adults are more capable at solving learning tasks than juveniles (Edwards & Jackson 1994, Skow & Jakob 2005, Hill 2006), this suggests that they may require experience to develop attentional skills for spatial tasks. Spiders are strongly influenced by innate behaviour; however, cognitive skills are flexible enough for innate behaviours to be perfected (Forster 1977; Edwards & Jackson 1994, Bartos & Szczepko 2012). Thus, it is reasonable to expect better performance in adults than in subadults, but, unfortunately, few performance differences were observed. Nevertheless, males completed routes faster than subadults and females. The speed at

which males completed routes was surprising, as previous work indicates that females are more motivated than males in predation-based (Jackson & Wilcox 1990) or learning (reviewed in Jakob & Long 2016) tasks. Because of this, few studies of this type have included males, yet previous work (Aguilar-Arguello et al. 2019) and this study suggests that males may be more mobile than females, possibly because they actively search for mates at this life stage (Jackson & Pollard 1997), and this is something that should be considered in future work. We observed that males were more active than females and subadults, especially among *Trite* individuals, in which males tended to be more skittish (pers. obs.).

If salticids are motivated and capable of choosing and completing difficult detours in which visual contact with the goal is lost, we believe they will exhibit three key components. These are the initial heading (to some extent, as discussed below), their final choice coinciding with the initial heading, and the fact that they re-orient toward the goal during the detour. However, this combination appears to be cognitively challenging: only three *Marpissa* and 12 *Trite* performed all three, while 87% (n =101) of 116 spiders tested lacked at least one of these three components in their detour.

Although we predicted that spiders would be able to discriminate lures and associate their location with the goal platform while still on the starting platform, the proportion of decided spiders did not differ from that of undecided individuals in either species, nor was this affected by route. This suggests that either: 1. the initial heading is not a good indicator of decision-making regarding chosen route, or 2. that the initial heading indicates a decision, but is often unclear because spiders are not motivated enough to follow the entire route.

In relation to the first hypothesis, that initial heading is a poor indicator of decision-making regarding the chosen route, Tarsitano and Jackson (1994) observed that, while scanning, *Trite* (and *Portia*) first focusses on the goal and then fixates on the different components of the detour, making it difficult to determine a variable that depicts the chosen route during the scanning stage. Thus, decision-making may instead result from the information compiled during the entire scanning process, rather than relying on the last orientation in the scanning routine. If the initial heading is a poor indicator of decision-making, the number of orientations toward a given route may be more indicative of route choice. Our data support the idea that the number of orientations toward a goal during scanning may be a better indicator of choice than initial heading, although how this works is presently unclear. In *Marpissa,* route completion was higher among spiders that performed a high number of orientations, while in *Trite* both the number of orientations and re-orientations were lower for routes that were more frequently chosen.

Evidence for the second hypothesis, that the initial heading is a good decision indicator, is provided by Tarsitano's (2006) work, where *Portia* went to the platform on the same side as their initial heading ('decided') significantly more often than those 'undecided' spiders that changed sides from their initial heading (19 versus 7; $X^2 = 5.538$, $P = 0.019$; Chi-square test of independence). Our experiment provided limited support for this hypothesis: for both species, but especially among *Trite*, the ratio of decided/undecided spiders did not differ, suggesting that initial heading alone is not always a good predictor of chosen outcome.

Inability to discriminate the presence or absence of prey seems unlikely as an explanation for our observed lack of route preferences. Goal platforms were 17 cm away from the starting platform and salticid vision is accurate within 30 cm (Jackson and Blest 1982). We also doubt that detour length was too challenging, as similar detour lengths have been tested, even with a hidden lure after leaving the starting platform (Tarsitano & Jackson 1997 = 139 cm, Cross & Jackson 2016 = 77.5 cm). However, previous successful experiments have been on *Portia* and other Spartaeine genera, which have exceptional cognitive ability among salticids (Jackson and Pollard 1996; Jackson and Cross 2011), and despite this, the execution of long detours with a hidden lure is difficult for *Portia* (Tarsitano & Jackson 1997). Non-spartaeines, including *Trite* and *Marpissa*, have performed well in detours up to 35 cm (Tarsitano & Jackson 1992), and *Trite* has completed 125 cm-long detours when a moving lure was visible throughout (Tarsitano & Jackson 1994). Possibly what made the present experiment especially difficult was that the lure was visible only from the starting platform, so spiders had to remember the goal's location.

Detouring requires the association of secondary objectives with the primary objective and the use of spatial memory to remember the exact location of the goal (Hill 1979), but visual input may require constantly updating (i.e., re-orientations) to keep motivated and maintain associations. Our data suggest that performing re-orientations is a strong indicator of motivation: *Marpissa* individuals that completed routes (34% of 61) re-oriented to the goal platform more often than those that did not (**Figure 3** in **APPENDIX 1**). In the case of complex detours, once visual contact with the goal is lost, the association between secondary and primary objectives may be severed, such that the spider cannot keep track of the detour. However, *Portia* and a few Spartaeinae species can follow long and intricate detours without the need to constantly update the primary goal's location (Jackson & Wilcox 1993) and without experience (Tarsitano & Jackson 1997, Cross & Jackson 2016). In contrast, non-spartaeines (including *Trite* and *Marpissa*) can only solve spatial tasks with visual access to a moving prey or when they have had previous experience (Nakamura & Yamashita 2000, Skow & Jakob 2005, Hill 2006, VanderSal & Hebets 2007, Liedtke & Schneider 2014). Coupling results from those previous studies and ours, we suggest that the

species used here can also perform detours as complex as those made by *Portia*, but may require experience to achieve this demanding spatial task. What it is surprising in *Portia* is its ability to plan ahead of time, and its ability to associate visual cues without previous experience. This could be unique not only among salticids, but among invertebrates.

Variation in spatial performance across salticid species is known. For example, despite its ability to complete different types of simple detours (Hill 1979), *Phidippus audax* failed in detours that required initially moving away from the goal for the correct detour (reverse-route detours; Carducci and Jakob 2000), which can be solved by *Trite* (Tarsitano & Jackson 1994). This variation in spatial ability has been attributed to the environmental structure in which each species lives (Tarsitano & Andrew 1999), with complex habitats presenting a more cognitively challenging navigational milieu (Gauin & FitzGerald 1986, Costanzo et al. 2009, Schwarz & Cheng 2010; Clarin et al. 2013, Schultheiss et al. 2016). The relationship between habitat attributes with performance in our study species fits this model, although significantly more comparative work in this area is needed. For instance, *Marpissa*'s struggle to complete the route may be a consequence of the lack of vertical routes in their natural environment, which primarily consists of small rounded rocks and a few pieces of driftwood. All *Trite* completed the routes and performed faster than *Marpissa*, which may be facilitated by adaptations to navigate within the vertical flax leaves that characterise its habitat.

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CHAPTER THREE. Risk assessment and the use of novel shortcuts in spatial detouring tasks in jumping spiders

Portia fimbriata scanning during one of the pool tasks.

Abstract

Selection on individuals that incorporate risk to quickly and accurately make *a priori* navigational assessments may lead to increased spatial ability. Jumping spiders (Araneae: Salticidae) are characterised by their highly acute vision, which mediates many behaviours, including prey capture and navigation. When moving to a specific goal (prey, nest, a potential mate, etc.), salticids rely on visual cues and spatial memory to orient in three-dimensional space. Salticid spatial ability has been studied in homing and detour tasks, with *Portia* being considered one of the most skilful genera in terms of spatial ability in the family. Commonly living in complex environments, salticids are likely to encounter a wide variety of routes that could lead to a goal, and, as selection favours individuals that can more quickly and accurately make assessments, they may be able to assess alternative route distances to select the most efficient route. Here, we tested whether two salticid species (*Portia fimbriata* and *Trite planiceps*) can discriminate and assess between different available routes by their length, and riskiness to escape from a stressful scenario. Results suggest that while *Portia* is more likely to choose the easiest and shortest escape routes, *Trite* is faster in both decision-making about which route to take, and to escape. However, some individuals were able to use novel shortcut routes instead of the routes expected, with *Portia* containing a higher proportion of shortcut-takers than *Trite*. These differences in spatial ability seem to correspond with the environmental complexity inhabited by each species.

Introduction

Assessment is the process by which animals evaluate perceived stimuli, converting them to an informational state to determine a specific level of risk or benefit (Blumstein & Bouskila 1996), while decision-making is a cognitive process that allows animals to evaluate their environment, so they can avoid less favorable situations. Thus, decision-making follows assessment and precedes observable behavior (Blumstein & Bouskila 1996). Because of increased ability to take the most efficient route to a goal, selection favours those individuals that can more quickly and accurately make assessments (Helfman 1989, Lima & Bednekoff 1999, Mirza & Chivers 2001, Brown 2003, Golub & Brown 2003). For example, in a food gathering task, selection of inefficient routes results in prolonged foraging, higher energetic cost, decreased time spent on other activities, and increased predation risk (Gibson et al. 2007).

Efficient route use has been observed in bees that integrate information about flight path vectors ('path integration') to navigate to the colony or a food source (Cartwright & Collett 1983), allowing them to make novel shortcuts, even if they cannot see the goal (Dyer 1991, Menzel et al.

2005, 2011). Similarly, shortcuts have been observed in desert ants (Wehner & Wehner 1990) and wandering spiders (Seyfarth et al. 1982). In these cases, proprioceptive mechanisms are used, and the distance assessment of the alternative routes is only done after experience. Here, we investigate whether invertebrates with no previous experience can assess different routes beforehand and follow the most efficient route to reach a goal, without the use of path integration.

Animals that pounce on their prey, such as jumping spiders (Salticidae), are ideal subjects to investigate decision-making. Salticids have a highly-developed visual system (Land et al. 2012) and perform precision jumps for predation and locomotion, accurately assessing the distance to the landing point (Nabawy et al. 2018). Furthermore, when a salticid identifies a prey, it is sometimes forced to take a detour, as the direct route is either inaccessible (Tarsitano & Jackson 1997), or disadvantageous (Jackson & Pollard 1996, Jackson & Wilcox 1993). Salticid detours are preceded by scanning behaviour which is characterised by a systematic movement of the body in order to visually inspect its surroundings (Tarsitano & Andrew 1999). Scanning is useful for visual inspection and route selection, but is also a crucial stage for navigation, as the individual potentially plans the route ahead of time (Cross & Jackson 2016). Previous detour-related tasks have shown that salticids can discriminate between routes that lead to a moving or non-moving prey item from routes that do not (Tarsitano & Jackson 1992, 1994, 1997, Tarsitano & Andrew 1999, Tarsitano 2006).

Commonly living in complex environments, salticid ability to find the best route out of a vast number of alternative pathways could be crucial to save energy and time, and avoid predation. Therefore, salticids may be able to assess, beforehand, alternative routes to select the optimum route. While detouring is a spatial ability apparently widespread among the Salticidae, there is a particular genus that stands out due to its exceptional cognitive abilities and its behavioural flexibility (Jackson & Pollard 1996, Jackson and Cross 2011). *Portia* lives in complex rainforest habitats in which it preys upon spiders (Jackson & Wilcox 1990, Harland & Jackson 2000). To reach prey, *Portia* can perform complex detours spanning over a meter, while losing sight of its prey for more than 80 min (Jackson & Hallas 1986a, Jackson & Wilcox 1993). This suggests not only an outstanding sense of orientation in three-dimensional space, but also spatial memory due to the spider's need to move out of line-of-sight of the prey to follow the detour.

Here, our main objective was to determine if salticids can *a priori* assess route distance and riskiness, but our study differs from previous work in that there was no clear best goal (e.g., prey) which was reached by a single correct route; rather the goal itself was to choose the most efficient (or least risky) way out of a stressful situation. Our routes were also discontinuous, being made up of dowels, such that the problem may be conceived of as a series of sub-goals which needed to be

connected in advance in order to achieve the least risky outcome (escape) which was, in itself, identical for all routes. We first tested if salticids differentiate the distance between the dowels and choose a route representing the safest option. Secondly, we tested whether they can discriminate between different routes according to length, and choose the most suitable one in order to escape a stressful scenario. Additionally, we explored whether there are intraspecific and interspecific differences in route assessment. Being from a complex habitat (Jackson & Blest 1982), and known for its cognitive ability (Jackson & Pollard 1996, Jackson & Cross 2011), we predicted that *Portia fimbriata* would be more effective at making efficient route choices compared with a salticid from a less complex habitat and not known for exceptional cognitive ability, *Trite planiceps*. Our prediction is based on the clever foraging hypothesis, which postulates that individuals living in more complex environments have better neurobiological navigational abilities (Striedter 2005, Park & Bell 2010). As salticid performance improves with knowledge about the environment (Edwards & Jackson 1994, Aguilar-Arguello et al. 2018), we also predicted that adults would outperform subadults. Additionally, we predicted that females would outperform males, as they are typically the more motivated sex, at least in predation-based or learning tasks (Jackson & Wilcox 1990, Jackson & Pollard 1996, Jakob & Long 2016).

Methods

Test animals and maintenance

Experiments were carried out from 0800 to 1300 h in the laboratory at the University of Canterbury. *Trite planiceps* Simon is a large (6-13 mm) salticid endemic to New Zealand and is typically found in coastal areas where it inhabits the rolled-up flax leaves of *Phormium tenux* and *Cordyline* spp. (Forster 1979). *T. planiceps* were field-collected in Christchurch, and were transferred to the laboratory, where they were housed individually in 1 L transparent plastic containers. Individuals were held in captivity for at least one week before testing. Spiders were fed once a week with two adult *Musca domestica*. Water supply was available through a cotton wick submerged in water which protruded into the container.

Portia fimbriata Doleschall is a large (6-11 mm) salticid from the rainforests of Northern Australia (Jackson & Hallas 1986a). *P. fimbriata* were lab-reared and, being predominantly araneophagic (spider-eating), were fed a combination of *Musca domestica* and a *Badumna longinqua* spider once a week. Individuals were housed as above.

Test arena

Salticid aversion to water is frequently used as a motivational tool in detour experiments (Cross and Jackson 2016). Here our aim was for spiders to choose a route to escape the stressful scenario of being surrounded by water by getting to the platform edge, rather than choosing a route to a specific target goal, such as prey. Our trials were performed in a 43 x 43 x 7 cm plastic container (pool) filled with water to a depth of 6 cm. From a central starting platform (PVC dowel, 9 cm high x 3.5 cm diameter) four possible escape routes extended to each of the four sides of the pool. Escape routes consisted of a series of PVC dowels (7 cm high x 1 cm diameter) protruding 1 cm from the water. These led to identical high-resolution pictures of foliage which surrounded the pool to both motivate the spiders to exit the pool and to provide visual obstruction of external visual stimuli. To account for directional biases, we rotated the pool to face North, South, West, or East at every trial. Rotations were randomised in blocks, each containing the four directions assigned in random order. To begin each trial, we gently placed a spider on the starting platform with a paintbrush. Spiders always rotated to observe their surroundings for between 50 to 220 s (1st and 3rd quartile) before choosing an escape route.

Each trial lasted up to 60 min, except if a spider was still on a route at this time, in which case we continued the trial until the spider reached the edge (maximum time: 110 min). If 60 min elapsed without the spider leaving the starting platform, the trial was aborted and the spider was re-tested (up to four times/day). In the rare cases in which the spider jumped into the water or missed a safe landing, we relocated it with a paintbrush to the dowel from which it had jumped. Relocation was only allowed twice during each trial; otherwise the individual was tested at a later date.

All trials were recorded with a webcam (Logitech C920 HD Pro) placed over the arena. The variables scored from video were route duration (time from leaving the platform to reaching an edge by using a route), the chosen route, the number of dowels used to reach the edge of the pool (as sometimes the spiders skipped dowels by jumping over the top of one), latency (elapsed time from the start of the trial to the beginning of scanning), and scanning duration (elapsed time from start of visual scanning to jumping off the starting platform). All analyses were done using R version 3.3.3 (R Core Team 2018).

Experiment 1

Our objective was to determine if salticids are able to discriminate a 'safe' route from three identical but more difficult 'risky' routes, and if performance at this task differs depending on species and spider age and sex category (see **APPENDIX 2.1**). Based on typical salticid jumps

being between 1-3 cm, the risky routes consisted of four dowels separated by 3.5 cm (centre to centre), while the fourth, safe route, was the same length but contained eight dowels separated by 1.75 cm, which is close enough for spiders to carefully walk across without jumping (**Figure 1A**). We tested 47 *Trite* (15 males, 18 females, and 14 subadults) and 62 *Portia* individuals (16 males, 19 females, and 27 subadults) and only analysed data from completed routes (see **APPENDIX 2.1**; **Figures 1,2 in APPENDIX 2**).

To ensure that the position of the dowels were placed at distances that spiders were able to differentiate, we recorded the number of dowels used when the spiders were escaping from the pool. Apart from the probability to choose a specific route, the proportion of dowels used during escape is important because there may be specific differences in jump length. These could alter the perceived difficulty of the routes, under three scenarios: 1. If the maximum separation between dowels in the risky routes is too small, we should expect no difference in route choice and also a low proportion of dowels used in both route types. In other words, the risky routes would be as easy as the safe route, the spiders would frequently skip dowels, and routes would be chosen randomly. 2. If the separation distance between dowels in the risky route is too large, we should expect no escapes through risky routes that are too difficult, and the use of the safe route should be the only outcome. Moreover, while using the safe route, spiders would also use a high proportion of dowels. 3. Risky routes are more difficult than safe routes, but still doable. The ideal scenario is providing doable routes, but with different levels of difficulty, so the spiders will be able to identify the safe route from the risky route and then make decisions about which one to take. In this case, the number of safe choices should be higher than random and the proportion of used dowels should be similar and high for both route types.

To investigate if route choice affected whether spiders skipped dowels, we compared the proportion of dowels used with respect to the total number of dowels in the chosen route. For this, we used a GLM with a binomial distribution and an additional dispersion parameter (family = quasibinomial) to account for over-dispersion. The proportion of dowels used was the response variable, with species, spider category (male, female, or subadult), the chosen route (safe or risky), and pool direction as the explanatory variables. The model accounted for all second-order interactions, but not for third-order interactions.

To determine if the spiders had a preference to choose the safe route, we used a GLM with a binomial distribution. Here, choice type (1 = safe route, 0 = risky route) was the binary response variable, while species and spider categories were the explanatory variables, accounting for second-order interactions. Given the estimated parameters, we calculated the confidence intervals (CI) of the observed choice type proportions for each species:spider category

combination. Whenever the lower limit of the CI was greater than the 0.25 proportion of random choice, we interpreted the spiders of such a group as significantly choosing the safe route more often than by chance at a confidence level of 95%. In the case of specific comparisons of subcategories within each explanatory variable, we used Wald tests or contrasts tests with the 'gmodels' package (Warnes et al. 2015); 95% CI were calculated for all estimated parameters.

Survival analyses, using Accelerated Failure Time models (AFT), were applied to scanning duration and route duration variables (Fox 2001). To select the best model, we used the Akaike Information Criterion (AIC; Crawley 2007).

Experiment 2

Our purpose was to determine if salticids can differentiate between different escape routes depending on their length, and if performance at this task differs depending on species and sex/age category. For these tests, methods were as described in Experiment 1, except for the configuration of the pool arena (**Figure 1B**). Here, spiders had to choose one of four different routes varying in length and number of dowels, with a straight route (4 dowels; maximum of 5 jumps to reach the pool edge), a zig-zag route (5 dowels; 6 jumps), a diagonal route (6 dowels; 7 jumps), and a curved route (7 dowels; 8 jumps). All dowels within all routes were separated by 3.5 cm. As a consequence, the energetically less expensive and shortest route was the straight route. We tested 42 *Trite* (11 males, 15 females, and 16 subadults), and 58 *Portia* (14 males, 19 females, and 25 subadults). All *Portia* tested had been tested in Experiment 1, while 23 of the 58 *Trite* were used in Experiment 1 and 35 *Trite* had been recently collected shortly before Experiment 2.

Recorded variables were as in Experiment 1, with some additions, as spiders did not always use all dowels of the chosen route to escape. Skipping dowels on the chosen route meant less jumps than expected for that route and a shorter or potentially easier route for the spiders, contrary to the objective of the experiment, as a spider skipping dowels (i.e., taking a shortcut) could potentially find a relatively easy way to escape even if it chose the longer route. To account for this behaviour, we calculated the number of dowels used by the spider divided by the number of dowels within the chosen route, with 1 meaning that the spider used all the available dowels in the escape route. We then included a binomial variable named 'shortcut-taking' to separate spiders that took shortcuts ($\leqq$ 0.75; labelled as 1), from spiders that did not ($>$ 0.75, labelled as 0). The threshold was set at 0.75 because taking shortcuts in the 6 and 7-dowel routes was almost unavoidable, as the last dowels were only 1 cm from the pool's edge and the spiders seldom used these dowels to reach the edge.

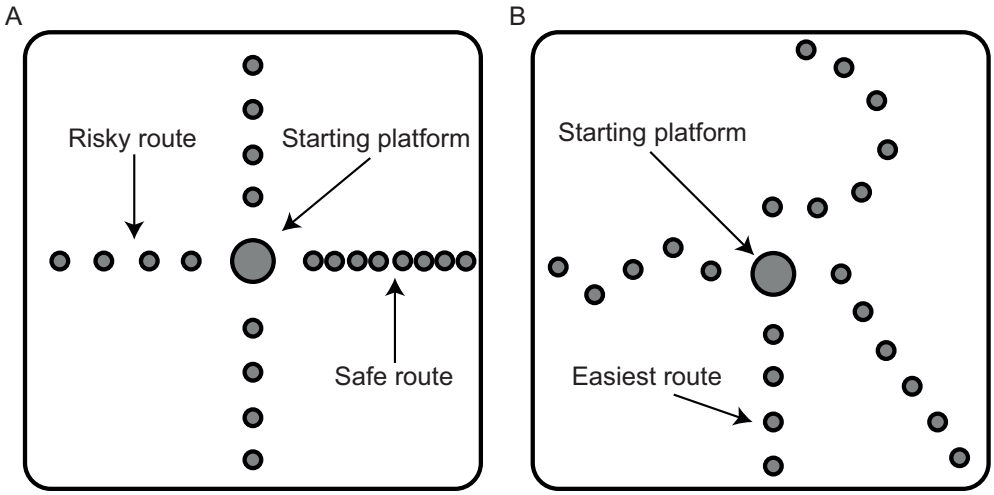

Figure 1. Test arenas for (**A**) Experiment 1; one safe versus three identical risky escape routes (dowel separation denotes risk level), and (**B**) Experiment 2; easy versus increasingly long routes. See methods for further details.

Shortcut-taking by the spiders to escape the arena was unexpected and exposed a potential flaw in our experimental design, as route preferences could be biased by spiders that took shortcuts. As a consequence, we performed two analyses; the first considering all data, and the second considering only data from non-shortcut-taking spiders. Analyzing both datasets separately not only assessed the behavior of all spiders and non-shortcut-taking spiders, but also allowed us to compare both datasets and make inferences about the effect of the explanatory variables among spiders that took shortcuts.

To test if there was a preference for a specific route depending on different response variables, we used two ordinal logistic regressions: for all data and for non-shortcut-taking spiders only. The chosen route was then parameterized as a 4-level ordered categorical response term (according to increasing number of dowels) in a cumulative link (or proportional odds) model (CLM, package: ordinal, Christensen 2018), with the terms spider category, species, and bout duration. Second-order interactions among the explanatory variables were not accounted for, as the AIC value was higher than the selected model. Wald and Likelihood test values were calculated for both CLM models. To make inferences about route preferences for *Portia* and *Trite*, we estimated the cumulative probabilities (*P*) to choose the different routes ordered by length at the intercept (when route duration is equal 0), and their CI at 95% (see **APPENDIX 2.2**). Thus, a preference to choose the 4-dowel route would be shown if *P* for 4-dowel route was >0.25. A preference for the 5 and 4-dowel route over the 6 and 7-dowel routes would exist if *P* >0.5, and a preference for using the 6-dowel route or shorter over the 7-dowel route would be shown when *P* >0.75.

Selection of the CLM including all data was the one with the lowest AIC value when checked for model diagnostics (see Christensen 2015). For comparative purposes, we used the same structure to analyse data from non-shortcut-taking spiders, so model selection was not used in this case. This model had the chosen route as the response variable, with spider category, species, and bout duration as explanatory variables, without interactions.

For both datasets, we analysed scanning duration and route duration using AFT survival models and we selected the distribution type based on the lowest AIC. For the response variable scanning duration, species, chosen route and shortcut-taking were the explanatory variables. Second-order interactions among the explanatory variables were not accounted for, as the AIC value was higher than the selected model. For the response variable route duration, species and chosen route were the explanatory variables.

To compare the number of shortcut-taking spiders versus non-shortcut-taking spiders, we used Chi-square tests of independence. The CLM was discarded as an option to analyse route choice, as the 'ordinal' nature of this variable is lost and the route choice is biased. In other words, taking shortcuts allowed spiders to take any route and make it novel, invalidating route length and violating the assumptions of ordinal logistic regression (Christensen 2015). Therefore, inferences about route preference were obtained from comparisons of CLM's belonging to general data and non-shortcut-taking spiders only. To compare the scanning duration and route duration among shortcut-taking spiders we used non-parametric Mann-Whitney and Kruskal-Wallis tests.

Results

Experiment 1

In our analysis of whether route choice affected if spiders skipped dowels, we found that the proportions of dowels used did not differ between spider categories, either for the chosen route or cardinal direction. The proportion of dowels used in risky (min, max, median; 25-75% quartiles; 0.25, 1.0, 1.0; 0.75-1.0) and safe routes (0.125, 1.0, 0.813; 0.5-1.0) was high, but was significantly higher for the risky routes ($U = 905.5$; $P = 0.02$). Additionally, *Trite* (0.5, 1.0, 1.0; 0.75-1.0) used a significantly higher proportion of available dowels ($U = 867.5$; $P < 0.0001$) than *Portia* (0.125, 1.0, 0.75; 0.47-1.0). Overall, we found no significant interactions between explanatory variables (see **Table 1** in **APPENDIX 2** for estimated effect sizes).

In *Portia*, the probability to choose risky routes was about 50% (**Figure 3** in **APPENDIX 2**), while *Trite* showed no preference for the safe route (**Figure 4** in **APPENDIX 2**). As a result, we were confident that the spatial task of experiment 1 was challenging, but achievable, for both

salticid agility and cognitive ability. *Portia* females (estimate; CIs reported for all) (0.47; 0.26-0.69) chose the safe route more often than expected by chance, whereas subadults (0.41; 0.24-0.59) and males (0.31; 0.13-0.56) chose the safe route with similar frequencies as the rest of the routes (**Figure 3** in **APPENDIX 2**). *Trite* females (0.22; 0.07-0.44) and subadults (0.21; 0.06-0.47) exhibited random route choice, while males (0; No data-1) never selected the safe route (**Figure 4** in **APPENDIX 2**).

Our survival analyses examined time to event data to estimate the effects of covariates on acceleration/deceleration of the survival time (in this particular case, the time in which the spiders end a determined behavioural stage, influenced by an explanatory variable). Explanatory variables were: chosen route, species, and spider category. All second-order interactions were also accounted for in this model. Because salticid scanning is thought to be crucial for navigational planning (Cross & Jackson 2016), we analysed the time spent scanning. *Portia* was equally likely to keep scanning over time, regardless of route chosen, although as time went on, the probability to remain scanning dropped (**Figure 2**). The latter effect was similar for *Trite*, but *Trite*'s probability to remain in scanning mode was higher when spiders opted to take the safe route compared with the risky routes (**Figure 2**). In other words, the probability to keep scanning during trials was significantly affected by the interaction of route choice and species, but not by route choice:category or category:species interactions (**Table 1**).

In terms of route duration, the AFT model was fitted to a lognormal distribution and chosen route:spider category, and species:spider category were the only interactions included. Spider category and species had a significant effect on the probability to remain on a chosen route. Specifically, *Portia* was more likely to stay *en route* than *Trite* (**Figure 5A** in **APPENDIX 2**), and females and subadults were more likely to stay on the chosen route than males (**Figure 5B** in **APPENDIX 2**). We found no significant interactions affecting route duration (**Table 2**).

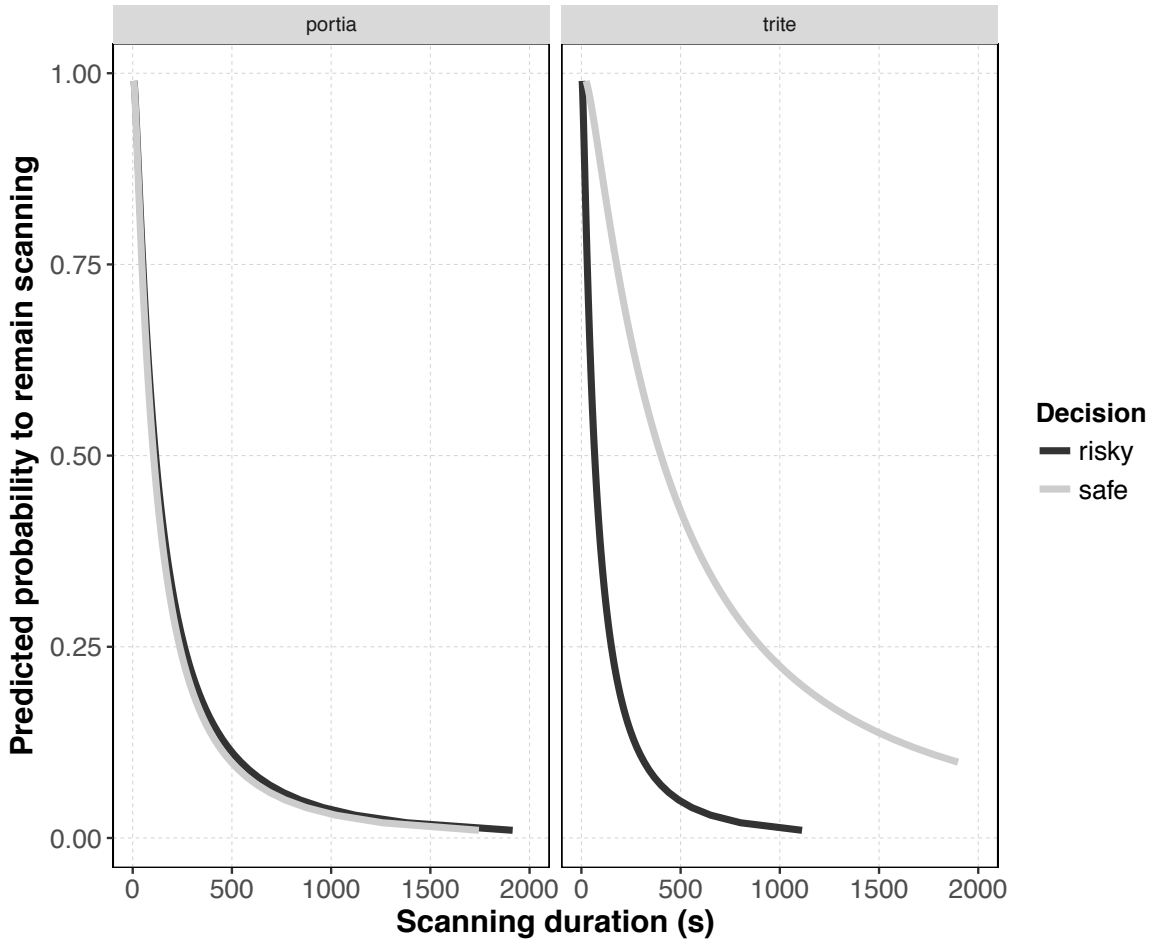

Figure 2. Accelerated Failure Time model curves depicting the probability of continuing scanning behaviour over time, as a factor of route chosen (risky or safe) in Experiment 1 for *Portia* and *Trite* spiders. *Portia*'s scanning behavior was not affected by route chosen, while *Trite*'s probability to remain in scanning mode was higher when spiders opted to take the safe route compared with the risky routes.

Table 1. Summary table of Accelerated Failure Time model with lognormal distribution: scanning duration as a function of route choice, spider category and species for Experiment 1, safe versus risky escape routes. Third order interactions were excluded. CI = confidence interval at 95%.

Variable	Estimate	CI	*Z*	*P*
Intercept	5.096	4.392 – 5.800	14.20	<2e-16
Route choice	-0.259	-1.223 – 0.705	-0.53	0.598
Species [*Trite*]	-0.877	-1.765 – 0.010	-1.94	0.052
Category [Subadult]	-0.244	-1.112 – 0.624	-0.55	0.581
Category [Male]	-0.819	-1.814 – 0.175	-1.61	0.106
Route choice: *Trite*	1.999	0.771 – 3.227	3.19	0.001
Route choice: Subadult	0.052	-1.102 – 1.206	0.09	0.929
Route choice: Male	0.325	-1.259 – 1.911	0.40	0.687
Subadult: *Trite*	0.274	-0.844 – 1.392	0.48	0.631
Male: *Trite*	0.757	-0.525 – 2.040	1.16	0.247
Log(scale)	0.174	NA	2.57	0.010

Table 2. Summary table of Accelerated Failure Time model with lognormal distribution: route duration as a function of route choice, spider category and species for Experiment 1, safe versus risky escape routes. Third order interactions and choice type: species interactions were excluded. CI = confidence interval at 95%.

Variable	Estimate	CI	*Z*	*P*
Intercept	5.553	5.051 – 6.055	21.67	<2e-16
Route choice	-0.508	-1.137 – 0.121	-1.58	0.113
Species [*Trite*]	-1.042	-1.642 – -0.441	-3.40	0.0006
Category [Subadult]	-0.458	-1.110 – 0.193	-1.38	0.168
Category [Male]	-0.912	-1.643 – -0.180	-2.44	0.014
Route choice: Subadult	0.181	-0.682 – 1.044	0.41	0.680
Route choice: Male	-0.547	-1.687 – 0.592	-0.94	0.346
Subadult: *Trite*	0.518	-0.325 – 1.361	1.20	0.228
Male: *Trite*	0.557	-0.365 – 1.479	1.18	0.236
Log(scale)	-0.106	NA	-1.57	0.116
Specific comparison				
Subadult vs Male	0.557	0.048 – 1.066	2.15	0.031

Experiment 2

When all data (shortcut-taking and non-shortcut-taking spiders) were included (**Table 3**), the selected CLM was built with the 'cloglog' link function. The probability of choosing a given route differed between species, with the odds of *Portia* choosing the 4-dowel route being 1.64 times that of *Trite*, which comparatively chose the longer routes. Spider category had no effect on the probability of choosing any given route, but route duration was related to the chosen route. In terms of odds ratios, a change of one unit (≡ 1 s) in route duration implies 0.07% increase in odds (0.7% for 10 s or 70% increase in odds for 1000 s) to choose the 5, 6, and 7-dowel routes instead of the 4-dowel route. This suggests that, when a spider took a long time to escape, it may have been simply because it chose a longer route instead of the 4-dowel route. In addition, *Portia* chose the 4-dowel route with a likelihood higher (P = 0.348) than the 0.25 expected by chance (CIs = 0.279, 0.425). The cumulative probability to choose either 4, 5 or 6-dowel routes was also lower than expected by chance in *Portia* (P = 0.688; CIs = 0.620, 0.749), meaning that the 7-dowel route was used more frequently than by chance. In the case of *Trite*, the cumulative probability to choose either the 4, 5 or 6-dowel route was lower than the 0.75 expected by chance (**Figure 3**), which indicates that *Trite* preferred the 7-dowel route over the rest of the routes (see **Table 2** in **APPENDIX 2**).

Table 3. Results of ordinal logistic regression model ('cloglog' link) for routes varying in difficulty for all spiders (spiders that skipped dowels, or took shortcuts, and non-shortcut-taking spiders) in Experiment 2. CI = confidence interval at 95% (estimates and CI of estimates from Wald tests).

Variable	Estimates	CI of estimate		Z	*P* Wald test	*P* likelihood ratio test	Odds Ratio	CI of odds ratio	
		2.5%	97.5%					2.5%	97.5%
Species	0.495	0.001	0.988	1.967	0.049	0.046	1.64	1.0	2.7
Category: subadult/female	-0.027	-0.573	0.518	-0.099	0.920	0.538*	NA	NA	
Category: male/female	-0.320	-0.927	0.286	-1.036	0.300				
Route duration	0.0007	0.0001	0.001	2.387	0.017	0.006	1.0007	1.0001	1.001

*the CLM likelihood ratio test estimates the effect of the spider category over the probability to choose each route chosen rather than compare pairs of sub groups (subadult vs female, male vs female) shown in the Wald test.

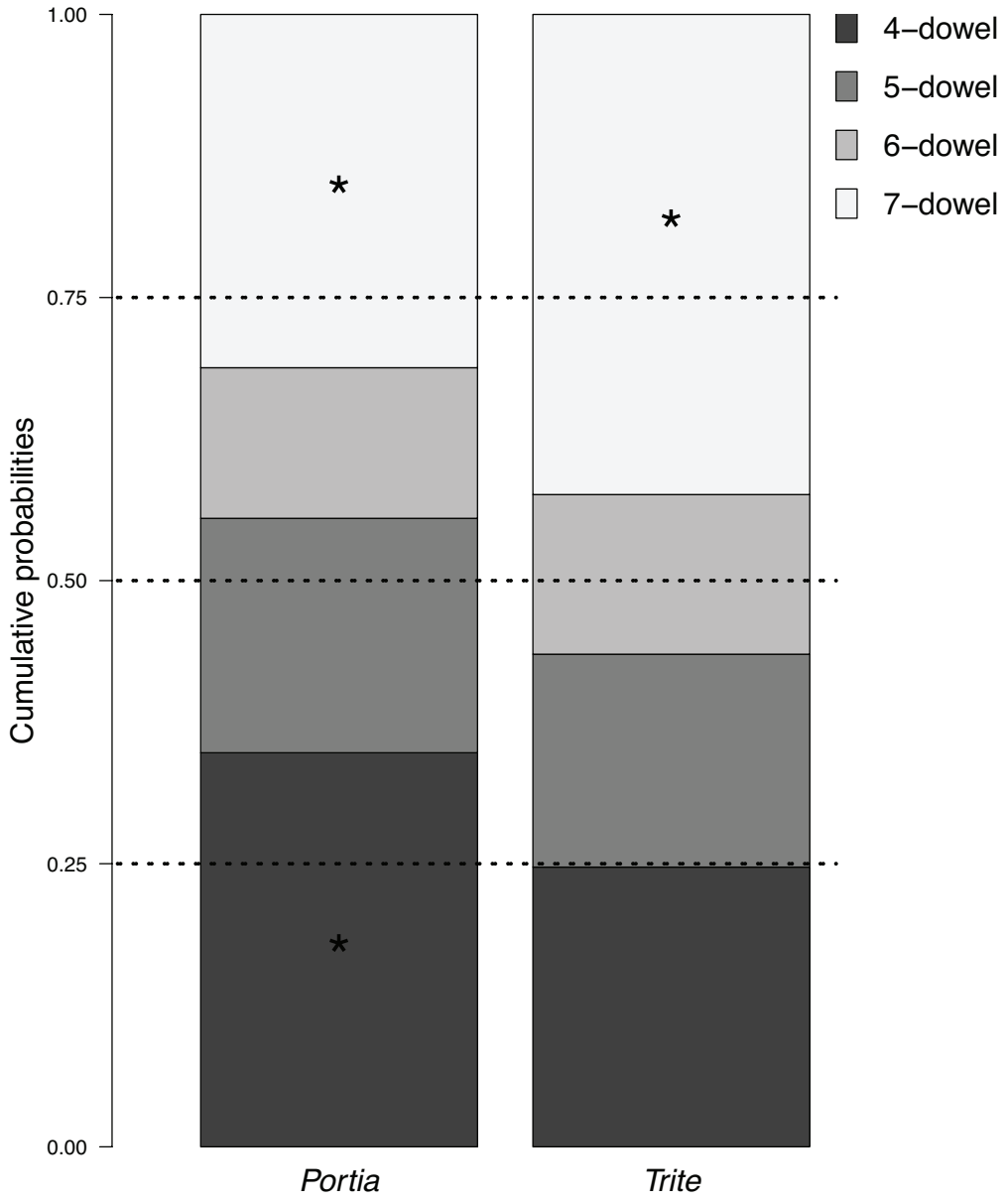

Figure 3. Cumulative probabilities for choosing routes by length calculated from the CLM considering all data set. Dotted lines depict the proportion of safe choices if spiders performed randomly (0.25 for 4-dowel, 0.5. for choosing either 4 or 5-dowel route, and 0.75 for choosing either 4,5, or 6-dowel routes). *denotes the use of each route with a frequency higher than by chance.

Furthermore, with the combined shortcut-taking and non-shortcut-taking data, we found no effect of spider species, chosen route, nor their interaction, on the probability to remain in scanning mode (**Table 4**). However, species had a significant effect on the probability to remain on a chosen route (**Table 5**), with *Portia* being more likely to remain *en route* than *Trite* (**Figure 4A**). Route length also significantly affected the probability of the spiders to remain on their chosen escape route, with the shorter (4 and 5-dowel) routes not differing, and having a significantly lower probability for spiders to remain (in other words, a higher probability to escape sooner) than when choosing the longer, 6 and 7-dowel, routes (**Table 5**, **Figure 4B**).

Table 4. Accelerated Failure Time (AFT) models fitted with loglogistic distribution for Experiment 2. The models include scanning duration as the response variable, whereas routes varying in length and spider species are considered as explanatory variables. The table shows AFT models results including all data (spiders that took shortcuts, and non-shortcut-taking spiders) and, below, for non-shortcut-taking spiders only. CI = confidence interval at 95%.

All data included				
Variable	Estimate	CI	*Z*	*P*
Intercept	5.199	4.684 – 5.714	19.79	<2e-16
Route [5-dowel]	-0.527	-1.294 – 0.239	-1.35	0.18
Route [6-dowel]	-0.287	-1.060 – 0.484	-0.73	0.47
Route [7-dowel]	-0.398	-1.236 – 0.440	-0.93	0.35
Species [*Trite*]	-0.504	-1.377 – 0.367	-1.13	0.26
5-dowel: *Trite*	0.406	-0.850 – 1.662	0.63	0.53
6-dowel: *Trite*	-0.343	-1.668 – 0.981	-0.51	0.61
7-dowel: *Trite*	-0.075	-1.312 – 1.162	-0.12	0.91
Log(scale)	-0.434	NA	-5.18	2.2e-07
Data from non-shortcut-taking spiders only				
Intercept	5.492	4.713 – 6.271	13.82	<2e-16
Route [5-dowel]	-0.075	-1.341 – 1.189	-0.12	0.906
Route [6-dowel]	-0.561	-2.137 – 1.014	-0.70	0.485
Route [7-dowel]	-0.546	-1.911 – 0.819	-0.78	0.433
Species [*Trite*]	-0.473	-1.620 – 0.674	-0.81	0.419
5-dowel: *Trite*	-0.205	-2.028 – 1.616	-0.22	0.825
6-dowel: *Trite*	-0.382	-2.687 – 1.921	-0.33	0.745
7-dowel: *Trite*	NA	NA	NA	NA
Log(scale)	-0.302	NA	-2.34	0.019

Table 5. Accelerated Failure Time (AFT) models fitted with lognormal distribution for Experiment 2. The models include route duration as the response variable, whereas routes varying in length and spider species are considered as explanatory variables. The table shows AFT models results including all data (spiders that took shortcuts, and non-shortcut-taking spiders) and, below, for non-shortcut-taking spiders only. CI = confidence interval at 95%.

All data included				
Comparisons	Estimate	CI	Z	*P*
Portia/*Trite*	-0.633	-1.031 – -0.235	-3.12	0.001
4-dowel/5-dowel	-0.005	-0.531 – 0.519	-0.02	0.982
4-dowel/6-dowel	0.572	0.001 – 1.143	1.96	0.049
4-dowel/7-dowel	0.779	0.261 – 1.296	2.95	0.003
5-dowel/6-dowel	0.578	-0.009 – 1.166	1.93	0.054
5-dowel/7-dowel	0.784	0.247 – 1.322	2.86	0.004
6-dowel/7-dowel	0.206	-0.381 – 0.794	0.69	0.490
Data from non-shortcut-taking spiders only				
Portia/*Trite*	-0.779	-1.333 – -0.224	-2.75	0.005
4-dowel/5-dowel	0.192	-0.425 – 0.809	0.61	0.541
4-dowel/6-dowel	0.898	0.108 – 1.688	2.23	0.025
4-dowel/7-dowel	0.217	-0.670 – 1.103	0.48	0.632
5-dowel/6-dowel	0.706	-0.148 – 1.560	1.62	0.103
5-dowel/7-dowel	0.024	-0.902 – 0.950	0.05	0.959
6-dowel/7-dowel	-0.682	-1.767 – 0.403	-1.23	0.218

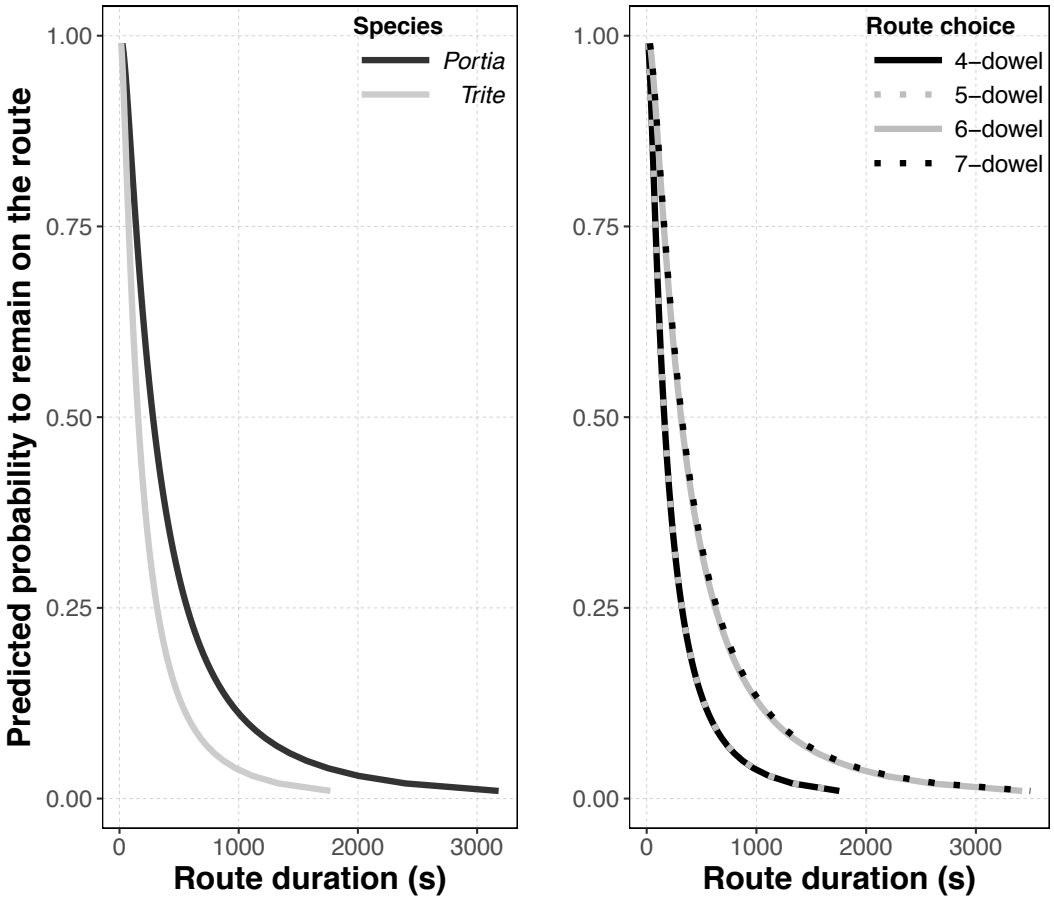

Figure 4. Accelerated Failure Time model curves for Experiment 2, depicting the probability of continuing on the route chosen over time for (**A**) all *Portia* and *Trite* spiders and (**B**) routes varying in length for both species combined (including data from spiders that skipped dowels, or took shortcuts, and those that did not).

When comparing shortcut-takers (39 *Portia* and 18 *Trite*) against non-shortcut-takers, (19 *Portia* and 24 *Trite*) we found that *Portia* was significantly more likely to skip dowels than *Trite* (X^2 = 5.91, P = 0.015; 67% versus 43%, respectively), however, no sex/age category within *Portia* was more likely to take shortcuts (X^2_2 = 0.262, P = 0.877; males: 71%, females: 63%, subadults: 68%). Within *Trite*, males (73%) were significantly more likely to take shortcuts than females (20%) or subadults (44%), although these are based on small sample sizes (X^2_2 = 7.21, P = 0.027) (see **Figure 6** in **APPENDIX 2** for sample sizes and trends).

We then partitioned the dataset to further explore trends within the shortcut-taking and non-shortcut-taking groups. The CLM for non-shortcut-taking spider dataset integrated the 'cloglog' link function, showing no significant effect of species, spider category, or route duration on the probability to choose a specific route (**Table 6**). Nevertheless, *Portia* chose the 4-dowel

route with a probability higher than the 0.25 expected by chance (P = 0.484; CIs = 0.364, 0.606; **Figure 5**), while *Trite* exhibited random route choices (see **Table 2** in **APPENDIX 2**). Similar to our results using the combined data (shortcut and non-shortcut-takers), we found that the probability of non-shortcut-taking spiders to remain scanning the chosen route was not affected by species, route chosen, nor their interaction (**Table 4**), that non-shortcut-taking *Portia* were more likely to remain on the chosen route than *Trite* (**Figure 7A** in **APPENDIX 2**), and that route length affected the probability of the spider remaining on that route (**Figure 7B** in **APPENDIX 2**; **Table 5**).

Within the subset of spiders that took shortcuts, we found no effect of sex/age category on scanning duration (H_2 = 3.367, P = 0.186) or route duration (H_2 = 1.889, P = 0.389) in *Portia* (**Figure 8A** in **APPENDIX 2**). Within *Trite*, however, while we found no effect of sex/age category on scanning duration (H_2 = 2.904, P = 0.234), we did find differences in route duration (H_2 = 6.934, P = 0.031; **Figure 8B** in **APPENDIX 2**), which were driven by female variability in a very small sample (n = 3 female shortcut-taking *Trite*) based on a single slow female, so this should be taken with caution.

Table 6. Results of ordinal logistic regression model ('cloglog' link) for spiders that took shortcuts in Experiment 2, for routes varying in length. CI = confidence interval at 95% (estimates and CI of estimates from Wald test).

Variable	Estimates	CI of estimate		Z	*P* Wald test	*P* likelihood ratio test	Odds Ratio	CI of odds ratio	
		2.5%	97.5%					2.5%	97.5%
Species	0.507	-0.271	1.28	1.276	0.202	0.203	1.66	0.8	3.6
Category: subadult/female	-0.242	-1.009	0.524	-0.620	0.536				
Category: male/female	-0.724	-1.815	0.366	-1.302	0.193	0.440	NA	NA	
Route duration	0.0001	-0.0005	0.0008	0.369	0.712	0.705	1.0001	0.8	3.6

*the CLM likelihood ratio test estimates the effect of the spider category over the probability to choose each route chosen rather than compare pairs of sub groups (subadult vs female, male vs female) shown in the Wald test.

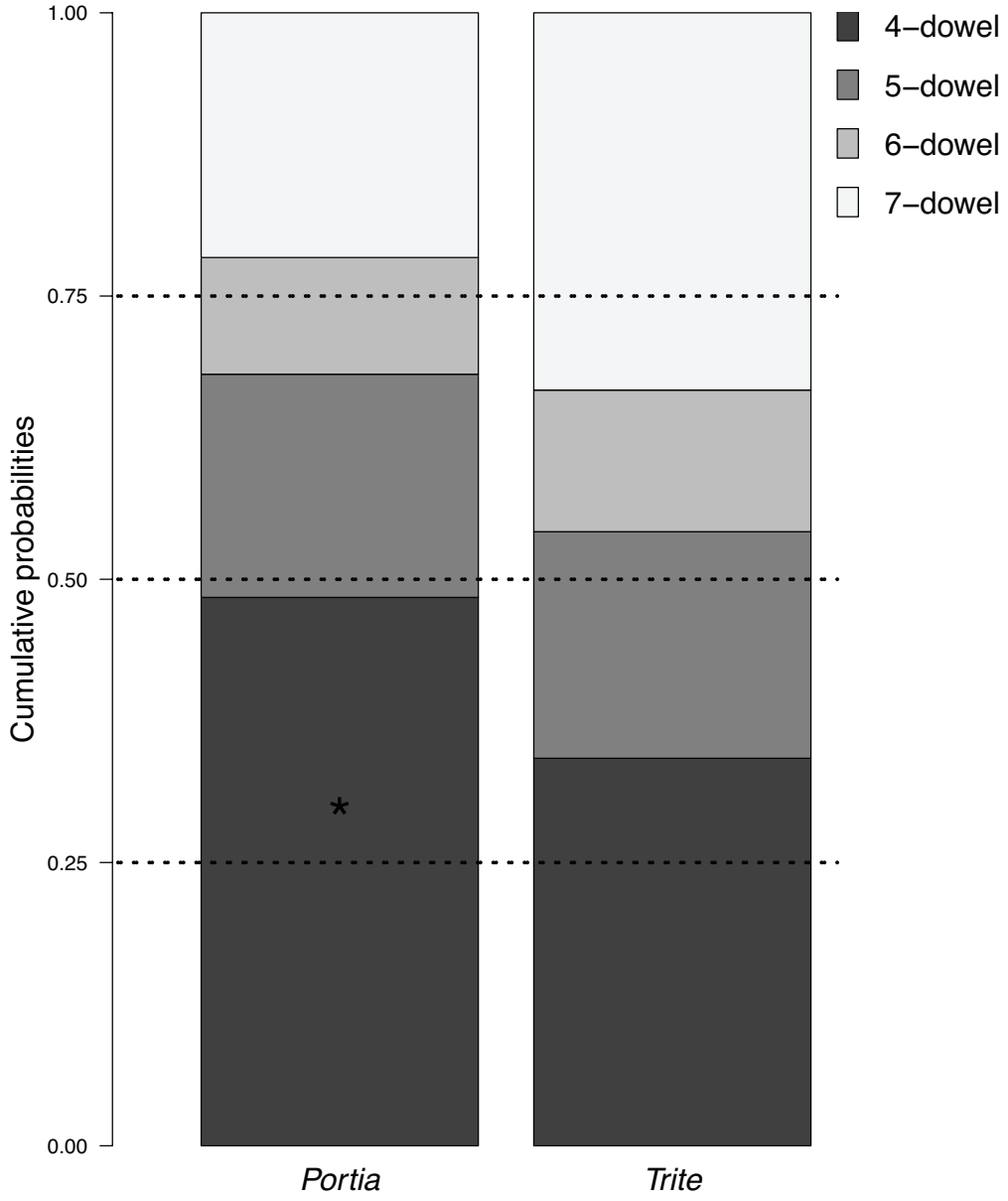

Figure 5. Cumulative probabilities for choosing routes by length calculated from the CLM considering non-shortcut-taking spiders. Dotted lines depict the proportion of safe choices if spiders performed randomly (0.25 for 4-dowel, 0.5. for choosing either 4 or 5-dowel route, and 0.75 for choosing either 4,5, or 6-dowel routes). *denotes the use of each route with a frequency higher than by chance.

Discussion

We demonstrate that salticids are able to assess distance in a spatial context by discriminating the difficulty of discontinuous routes. Furthermore, salticids can devise novel shortcuts or short route options to escape the testing arena. *Portia* was either more inclined to make larger jumps or better at assessing spatial tasks than Trite as evidenced by the preference of the safe escape route for Experiment 1, tending to take shortcuts more and preferring the shortest route when it did not take shortcuts in Experiment 2.

The physical difficulty of our tests in terms of distance between dowels is unlikely to have been overly challenging for either species. All individuals were able to jump from one dowel to another and all were able to escape from the pool, even using the most difficult routes (i.e., risky and 7-dowel routes). Both species have the ability to jump several times the distances used here (*Trite*: up to 150 mm (Taylor & Jackson 1999); *Portia*: up to 80 mm (Jackson & Hallas 1986b). Interspecific differences are thus likely to be either due to differences in rearing conditions (*Trite* were field collected, while *Portia* were lab-reared), spatial or cognitive ability, motivation, or a combination of both of the latter, rather than inability to escape through a difficult route.

Previous detour-related tasks on salticids, including the species tested here, show that they discriminate between routes leading to a prey item from those that do not (Tarsitano & Jackson 1992, 1994, 1997, Tarsitano & Andrew 1999, Tarsitano 2006). Unlike in those studies, we did not restrict our testing solely to adult females and there was no clear best goal at the end of a single correct route. Instead, the goal was to choose the most efficient, or least risky, escape from a stressful situation. Additionally, the routes were discontinuous, leading to the problem being conceptualized as a series of sub-goals or route attributes that had to be connected in advance to achieve the least risky outcome (escape) which was, in itself, identical for all routes. The location of a sub-goal (or secondary objective) must therefore be stored in memory (Hill 1979), and, as the number of sub-goals increases, more memory capacity is required. Thus, our tests should require more complex cognitive processing than continuous routes that lead or do not lead to a single salient outcome. Perhaps it is because of these differences that we found less clear-cut effects than previous studies (e.g., Tarsitano & Jackson 1992, 1994, 1997, Tarsitano & Andrew 1999, Tarsitano 2006).

While rearing salticids in a social environment (Leidtke & Schneider 2017) and with environmental enrichment (Carducci & Jakob 2000) makes them perform better in learning tasks, rearing condition does not seem to adequately explain our results. All spiders were housed with environmental enrichment, lab-reared spiders were reared socially for the first few instars of their life (*Portia* eat each other so this is not feasible for their entire life-span), and all tested spiders were

naïve to the apparatus. Our experience in rearing salticids has typically been that after several generations within the lab, salticids perform more poorly. Our *Portia* were 3rd generation lab-reared, yet outperformed wild-caught *Trite*. Another possibility to explain our results is that salticids were able to count the number of dowels forming an escape route, and make decisions based on this. It is known that a related species to *Portia fimbriata*, *P. africana*, can classify up to 3 prey as discrete number categories (Nelson & Jackson 2012, Cross & Jackson 2017). It remains unclear whether failure of higher numerical ability is a cognitive or motivational limitation. While the possibility that our spiders were able to count dowels is tantalizing, it is impossible to determine whether route preference was driven by the number of dowels within the route. Non-verbal ability to discretely count objects ('subitize') tends to break down above four (Gallistel & Gelman 2000, Dacke & Srinivasan 2008), which was the minimum number of dowels used in these tests. Thus, it is unlikely that our *P. fimbriata* could numerically distinguish between routes. Instead, these may have been assessed in terms of the 'quantity' of the continuous variables created by having more dowels (i.e., surface area, volume, areas of contrast, etc.). Our results indicate that *Portia* is likely able to assess a route by its length, and by the distance between dowels, and may be better able at evaluating a path containing multiple sub-goals (dowels) than *Trite*, which, in turn, may tend to assess only from one dowel to the next without searching for alternative sub-goals, resulting in less incidence of taking shortcuts.

Portia was generally slower at escaping the pool arena, possibly because it adopts an unusually slow, choppy, gait when walking (Jackson & Blest 1982, Jackson & Hallas 1986b). Nevertheless, several strands of evidence suggest that our experiments posed problems more easily solved by *Portia* than *Trite*: in Experiment 1, *Portia* took safe routes above chance levels, yet scanning duration for this species was similar for both safe and risky routes. In contrast, *Trite*'s route choice was random, but when it did choose the safe route, prior to exiting the starting platform it scanned the route longer compared with risky routes and compared with *Portia*. In salticids, the duration of visual scanning is correlated with decision-making and planning ahead of time (Cross & Jackson 2016, Tarsitano & Andrew 1999). This suggests either that *Portia* was more flexible and willing to take risks 'on the fly', or was faster at assessing its visual surroundings to make an 'informed' risk-averse decision compared with *Trite*. Furthermore, in Experiment 2, when using the entire dataset, *Portia* was more likely than *Trite* to escape via shorter routes. Additionally, for spiders that took shortcuts, decision-making in both species did not differ for the 5, 6, and 7-dowel routes, yet *Portia* preferred the 4-dowel route, while *Trite* showed no preference. Results of Experiment 1, in which *Portia* used a significantly lower proportion of dowels compared with *Trite,* corroborate findings of Experiment 2, in which *Portia* was significantly more likely to take

shortcuts than *Trite*. This may suggest that *Portia* has better facility to 'mentally' create shortcuts or assess easier routes than *Trite* (i.e., route planning, Cross & Jackson 2016). Our results are in line with a previous comparative detour task in which *Portia* exhibited better visual discrimination for non-moving prey than *Trite* (Tarsitano & Jackson 1994). Interestingly, when comparing results from data containing both spiders that took and did not take shortcuts with those that did not take shortcuts only, we found that spiders of both species that took shortcuts exhibited a preference for the 7-dowel route. As the longest route, we expected the 7-dowel route to be the less preferred option. It is possible that the shape of the route may have provided a wider range of alternative routes for spiders due to the curved arrangement of the dowels. This meant that, in practice, skipping dowels on the longest route required a shorter jump than skipping dowels on the other routes. Coupled with this, the angle as the route neared the pool edge meant that the distance to the edge from the 5th and 6th dowels was short, making it relatively easy to jump to the edge from these two dowels, thus skipping the 7th dowel.

Due to psychophysical and behavioural evidence that females are better performers than males (Jackson & Hallas 1986, Jackson & Pollard 1996, Jakob & Long 2016, Zurek et al. 2010, Zurek & Nelson 2012), we expected females to outperform males and subadults, and also that adults would outperform subadults, because experience seems to improve behavioural outcomes in salticids (Edwards & Jackson 1994, Skow & Jakob 2005, Hill 2006). Possibly because we used neither potential prey nor conspecifics (often used as motivators in salticid studies) in our tests, sex and age differences were not apparent in our cognitively-demanding experimental set-up, other than males tended to complete routes faster - possibly because adult males may be more active due to their role in actively searching for mates at this life stage (Jackson & Pollard 1997). The other exception, that shortcut-taking females were marginally slower to escape than males and subadults, should be taken with caution, as this was based on a single female (from three) that took a very long time.

Differences in spatial ability selected by characteristics of the environment have been observed in several taxa (Gauin & FitzGerald 1986, Costanzo et al. 2009, Schwarz & Cheng 2010, Clarin et al. 2013). For example, despite the fact that *Melophorus* sp. and *M. bagoti* are closely-related species of desert ants, they rely on different navigation mechanisms: *M. bagoti* inhabits visually-rich environments and depend mainly on visual landmarks for orientation, whereas *Melophorus* sp. lives in visually-barren environments (Schwarz & Cheng 2010, Schultheiss et al. 2016) and primarily relies on path integration. It is tempting, but premature, to conclude that the simpler environment inhabited by *Trite*, consisting of flax bushes to a height of about 2.5 m (Taylor & Jackson 1999), could lead to different spatial ability than *Portia*. Additionally, in the rainforest of Australia, *Portia*

has numerous predators and considerable competition for prey (Jackson & Blest 1982). In contrast, in the temperate areas of New Zealand, where *Trite* is found, there is significantly lower competition for food, and predation is most likely limited to birds and a few invertebrates, including dragonflies and earwigs, two parasitoid wasps, and three species of spider (Taylor 1997, Taylor & Jackson 1999). Tarsitano and Andrew (1999) proposed that *Portia*'s spatial prowess may be selected for as a consequence of having to search for mates or prey in a complex environment containing large trees (Jackson & Blest 1982), as suggested by the clever foraging hypothesis (Striedter 2005; Park & Bell 2010). To adequately answer this question, we must assess whether salticids can plan entire routes before leaving a starting platform, rather than making adjustments *en route*. Our findings about willingness to take shortcuts suggest that further refinements are needed to address whether interspecific differences in shortcut-taking are either due to premeditated decisions, or to interspecific differences in inclination to improvise during the execution of a given trajectory.

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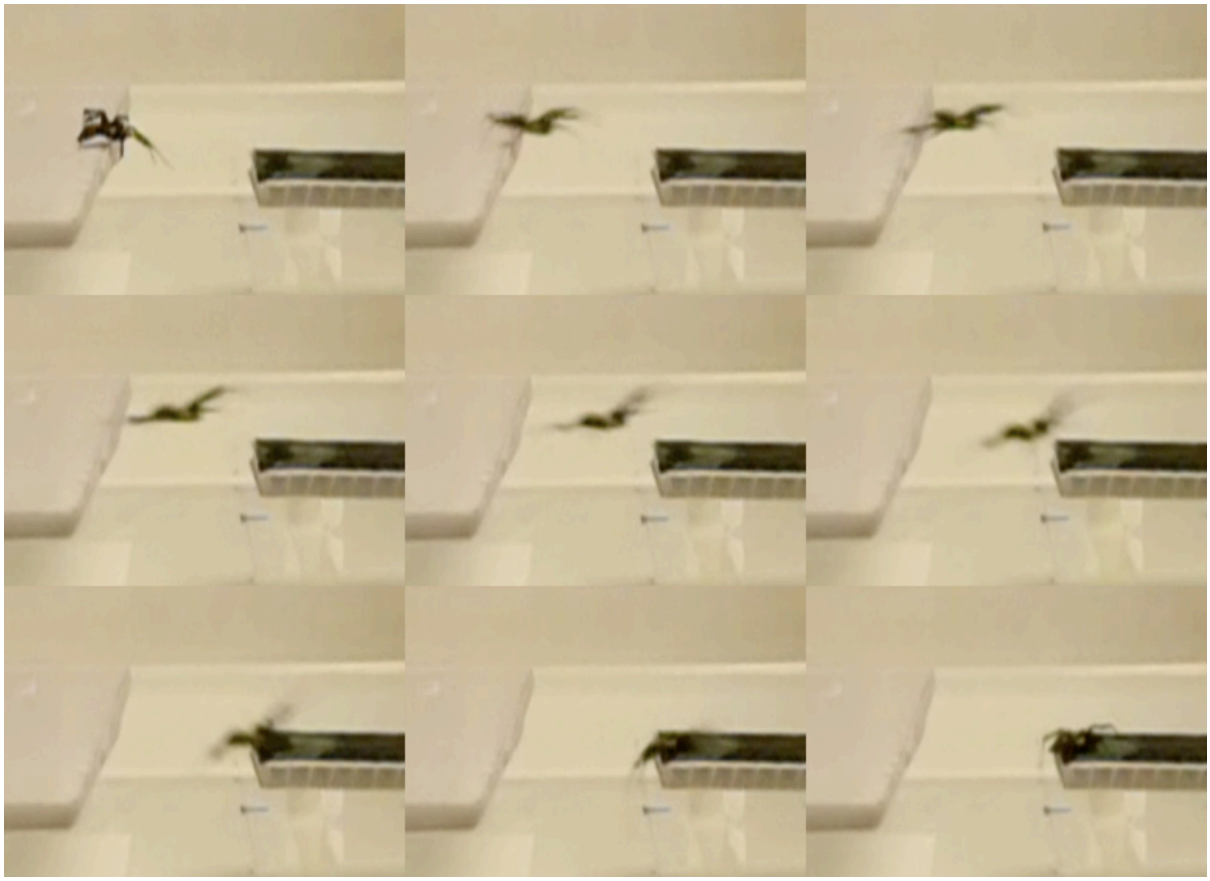
CHAPTER FOUR. Jumping spiders attend to information from multiple modalities when preparing to jump



Portia fimbriata performing a successful jump in a control trial.

Abstract

Animals often rely on different sources of information when making decisions about the environment. Here, we assessed whether two jumping spiders (Salticidae), *Trite planiceps* and *Portia fimbriata*, take into account two different sources of information when jumping over water, to which they are averse. Specifically, we investigated if salticids can assess both mechanical (wind) and visual cues while jumping from one platform within a pool arena to another. Initially, salticids were exposed to either no wind, low wind speed or high wind speed. Spiders adjusted the horizontal direction of the jump depending on wind presence. Prior to jumping, there was a tendency to move toward the wind source with increasing wind speed, such that the wind would favour the jump. Furthermore, independent of wind presence, the vertical trajectory of the jump affected jump outcome (success or failure) in *Portia*, but not in *Trite*. In a second experiment, salticids were exposed to intermittent wind in 10 s bouts to assess whether they preferred to jump during bouts without wind. As expected, spiders preferred to jump when there was no wind. Overall, we found that salticids do account for wind conditions when initiating a potentially risky jump.

Introduction

Animals often rely on different sources of information when making decisions about how they should behave in an environment (Sih 1992, Dall & Johnstone 2002). This awareness is crucial for behaviours that affect an individual's fitness, such as predator-prey interactions (Munoz & Blumstein 2012), male-male contests (McGinley et al. 2015), navigation (Grocott 2003), mating tactics (Dombrovsky & Perrin 1994, Getty 1996, Luttbeg 1996, Mazalov 1996), and foraging (Dall & Johnstone 2002). Given unlimited processing of information, the greater the number of different sources of information, the more accurate the assessment (Real 1992). However, with a finite nervous system, animals are constrained by their ability to process multiple sources of information simultaneously. Nevertheless, because their use permits an animal to assess its surroundings more accurately, many animals use multiple sources of sensory information when making decisions (Partan 2004, 2013). This is true not only of large-brained animals, like humans, whose grey matter in the cerebral cortex alone has roughly 14 billion neurons (von Bartheld et al. 2016), but even in those with minute brains, such as jumping spiders, whose brains are estimated to contain 500,000 neurons (Mike Land, pers. comm.), or in Cupiennius spiders, with an estimated 50,000 neurons (Barth 2002).

The use of cues or signals from multiple sensory modalities, including vision, chemoreception and mechanoreception, is used by spiders to assess mates or escape prey (Den Otter 1974, Barth 1993, Barth et al. 1995, Fenk et al. 2010, Hebets & Uetz, 1999, 2000, Roberts et al. 2006). For mechanoreception, spider legs are equipped with long hairs called trichobothria (Foelix 2011). Trichobothria are so sensitive that some spiders, such as Cupiennius, can detect the airflow of a buzzing fly up to 25 cm away (Barth et al. 1995), or the wind movement caused by prey walking 1-3 cm away (Den Otter 1974, ReifBland & Görner 1978). In addition, the use of both wind and substrate vibrations allows spiders to distinguish between an approaching prey and a potential threat (Barth et al. 1995). Wind perception in spiders is important for dispersal (Van Wingerden & Vugts 1974, Tolbert 1977, Duffey 1998), web-building (Liao et al. 2009, Wu et al. 2013), and predation (Hergenröder & Barth 1983, Coddington & Sobrevila 1987, Barth et al. 1995). Due to the sensitivity of the trichobothria, it is likely that perception of wind, in combination with other sensory modalities, is used to inform decisions in scenarios additional to those described above.

Jumping spiders (Salticidae) are active roaming predators that typically do not use webs to catch prey. They are able to detect, identify, and attack prey using their highly acute vision (Land 1969a,b, Harland et al. 2011). For salticids, vision is a key sensory modality that mediates several activities, including prey capture (Jackson 2000, Li et al. 2003), agonistic displays (Wells 1988, Taylor et al. 2001), courtship (Clark & Morjan 2001), and navigation (Hoefler & Jakob 2006). Despite their propensity to use vision, the use of chemosensory (Nelson et al. 2012) and mechanosensory (e.g., seismic) information is also known in this family, and decisions can be made on the basis of input from several modalities (Elias et al. 2003, 2008, 2010).

The use and detection of wind has been little studied in salticids, apart from some studies on *Portia*, spider-eating salticids that use gusts of wind to mask their own vibrations as they invade the webs of the spiders that they are hunting (smokescreen behaviour, Wilcox et al. 1996). Nevertheless, evidence suggests that salticids have sophisticated mechanosensory abilities (Shamble et al. 2016), and its use in behaviour is implied by studies in which salticids, such as *Trite planiceps*, attack prey in complete darkness. This is thought to be mediated by detecting the airflow emitted by the prey, rather than its odour (Forster 1982). In addition, salticids may rely on airborne mechanosensory cues to detect predators and potential mates (Shamble et al. 2016).

Aside from mechanical work on how salticid jumps are achieved (Parry & Brown 1959, Hill 2006, Nabawy et al. 2018), research into the behaviour that forms their namesake has been scant. Salticids can jump to escape from threats in an unprepared manner (which can be in any direction), but notably, salticids perform targeted jumps which are used to hunt prey or to move

through a discontinuous environment, such as between branches within a bush (Hill 2006, Weihmann et al. 2010). In targeted jumps, spiders estimate the relative distance and direction of the target, accounting for the effect of gravity on a jump (Hill 2006) and adjusting the trajectory of the jump according to the specific jumping task (Nabawy et al. 2018). However, whether salticids use sensory information other than vision to calculate the setup of their jumps has not been considered.

Wind is a common environmental factor that could significantly affect jump dynamics, especially when spiders are located far above the ground (e.g., in an overgrown grassland wind speeds reach 90 cm^{s-1} at 1 m height, Tolbert 1977), or when there is a lack of surrounding vegetation (e.g., up to 400 cm^{s-1} at 2 m height in dunes, Wingerden & Vugts 1974). This suggests that, especially in the case of targeted jumps, wind must be accounted for by the spider in order to successfully jump from one place to another. Here, our objective was to determine whether salticids can perceive and use wind-based information to initiate a jump, in addition to the use of vision. Using two species, *Portia fimbriata* Doleschall and *Trite planiceps* Simon, we predicted that, depending on wind speed, spiders would adjust their take-off position and jump trajectory. Thus, in high wind conditions, salticids would make fast, flat (less parabolic) jumps and would move upwind (i.e., closer to the source of wind), such that the jump would carry them downwind to the target, and that this would be especially evident in lighter spiders that may be displaced further by the wind. Additionally, previous work suggests that *Portia fimbriata* may have better spatial cognitive ability than *Trite planiceps* (Aguilar-Arguello et al. 2019, 2020), so we predicted that *Portia* would perform better than *Trite*. Due to differences in morphology and behaviour (Forster 1979, 1982, Jackson & Blest 1982, Jackson & Hallas 1986a,b, Taylor 1998, Taylor & Jackson 1999), we anticipated differences in jump mechanics between the two species. Finally, we predicted that, in an intermittent wind condition, spiders would tend to jump during periods without wind.

Methods

Test animals and maintenance

Trite planiceps is a large (6-13 mm) salticid endemic to New Zealand that is typically found in coastal areas, where it inhabits the rolled-up flax leaves of *Phormium tenax* and *Cordyline* spp. (Forster 1979). *Trite planiceps* were field-collected in Christchurch, and were transferred to the laboratory, where they were housed individually in 1 L transparent plastic containers. Individuals were held in captivity for at least one week before testing. Spiders were fed weekly with two adult

Musca domestica. Water supply was available through a cotton wick submerged in water which protruded into the housing container.

Portia fimbriata is a large (6-11 mm) salticid from the rainforests of Northern Australia (Jackson & Hallas 1986a,b). *Portia fimbriata* were lab-reared and, being predominantly a spider-eating species, were fed a combination of *Musca domestica* and a single *Badumna longinqua* spider once a week. Individuals were housed as above.

Test arena

Trials were performed in a plastic container (pool arena) filled with water to a height of 60 mm (see **Figure 1** for dimensions). Four identical high-resolution pictures of foliage surrounded the pool, providing motivation for the spiders to exit the pool and obstructing external visual stimuli. Within the pool there was a starting platform, raised 10 mm above the water level. A landing platform, raised 5 mm above the water level, was positioned between the pool edge and the starting platform, at a distance of 30 mm from the starting platform. Additionally, two PVC tubes were placed at either side of the arena: the wind tube (which directed the wind) and a control tube with the same features as the wind tube.

Wind was produced by two devices. To produce the low wind speed, we used two computer fans (120 mm diameter, 120 V) embedded in a box connected to the PVC tube to direct the airflow to the arena. High wind speed was achieved by attaching a leaf blower (Ryobi One+ 18 V Jet Blower) to the PVC tube. Both wind-blowing devices were connected to a power supply which allowed us to regulate wind speed. To determine our two wind speeds, we calculated the displacement of the spider when exposed to wind. For this, we hung five CO_2-sedated individuals of each species from their silken draglines in front of the wind pipe to measure the angle of displacement. We set the wind speed to displace the spiders by an angle of 30° for the low wind, and 60° for the high wind speed treatments. As individuals from both species were similarly displaced by wind, we used the same speeds for both species: low wind at 2.5 m^{s-1} and high wind at 5.5 m^{s-1}. During tests, wind direction (left to right or vv.) was randomised for each spider (i.e., repeated trials on the same spider had the same wind direction). Depending on the experiment, the wind was either constant (Experiment 1), or intermittent (Experiment 2). All experiments were carried out from 0800 to 1400 h in the laboratory at the University of Canterbury, New Zealand.

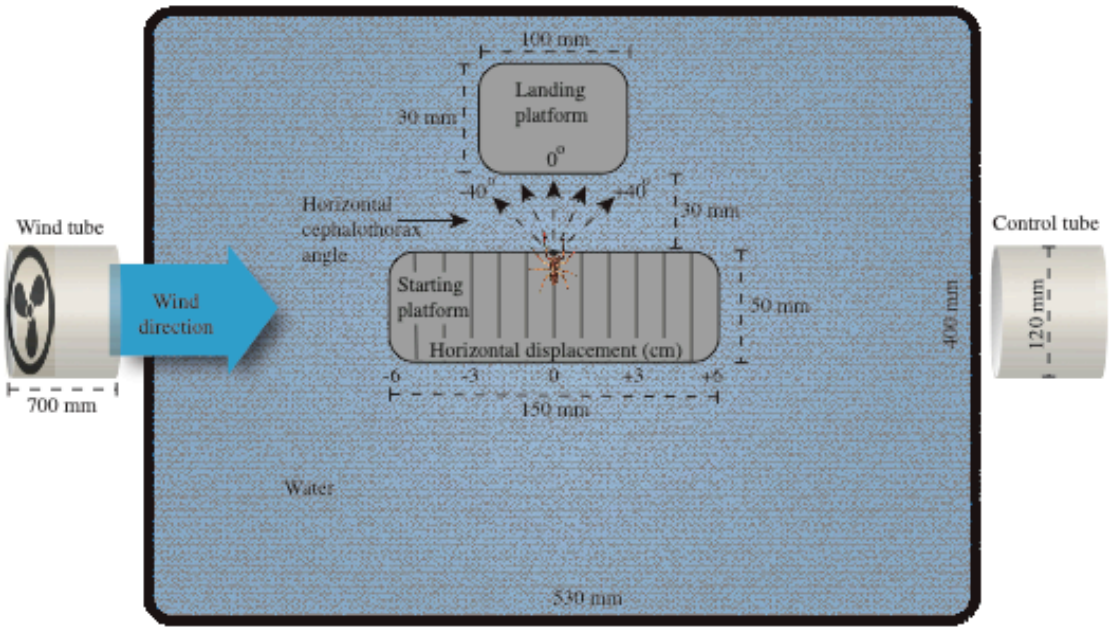


Figure 1. Test arena (95 mm deep pool) for testing salticids jumps in wind. Wind direction is depicted from left to right. Starting platform depicts the horizontal displacement (cm) of the spider relative to the centre of the platform (0). Negative distance represents horizontal displacement toward the wind direction. Positive displacement is recorded when the spider moves away from the wind pipe. The horizontal cephalothorax angle (degrees) represents the direction of the cephalothorax before the jump, with negative angles representing adjustments toward the direction of the wind. Figure not to scale.

Experiment 1

This experiment was performed to assess whether salticids account for wind presence and its speed to adjust their targeted jumps. The treatments were: i) control, in which control and wind tubes were present but the wind device was off, ii) low wind speed, in which the computer fan blew at a constant low wind speed, iii) high wind speed, in which the leaf blower blew at a constant high wind speed. Each test spider was tested in all treatments in random order. Because jumping from one platform to another in high wind was a difficult task, the maximum trial duration was 120 min. If spiders failed to make a jump in this time, they were re-tested at least 48 h later.

We tested 26 *Trite* (14 females, 3 subadults, and 9 males) and 11 *Portia females* in each of the three treatments (i.e., there were a maximum of 111 jump attempt possibilities: 26 *Trite* x 3 treatments plus 11 *Portia* x 3 treatments; however, in two instances spiders died before all three treatments had been performed). To examine the effect of the noise of the leaf blower, for control and low wind treatments, an additional 7 *Portia* and 23 *Trite* were tested with a speaker playing a

recording of the leaf blower at the equivalent sound level as in the high wind treatment (82.1 dB). We then examined the behaviours that were affected by wind treatment to determine the effect of noise. The noise produced by the leaf blower did somewhat affect spider behaviour, but not in most key parameters relating to jump trajectory (see **APPENDIX 3.1**).

Experiment 2

Here, the objective was to determine whether *Trite* (N = 35, 17 females, 9 males, and 9 subadults; note: no *Portia* were available when conducting this experiment) can account for wind presence to perform a jump, and whether, all other things being equal, spiders choose to jump in 'safer' non-windy conditions. The setup for this experiment was as in the high wind treatment in Experiment 1, with the caveat that we installed an openable hatch within the PVC tube in order to expose the spiders to intermittent wind conditions (i.e., when the hatch was open, wind was allowed through and across the test arena, but not when the hatch was closed). Thus, the leaf blower was turned on during the whole trial, but the hatch was automatically actioned by a switch every 10 s, enabling repeated bouts of 10 s without wind and 10 s with high wind. The condition in which the trial started (hatch open or closed) was such that half of the trials started with an open hatch and the other half started with the closed hatch, in random order. Maximum trial duration was 60 min. If spiders failed to make a jump in this time, they were re-tested at least 48 h later.

Data analyses

Trials were recorded from above using a webcam (Logitech c 920 HD Pro, 30 fps), and also from the side with a digital camera (Panasonic LUMIX TZ90) at 200 fps with 640 x 480 resolution. Videos were then scored and analysed.

For Experiment 1, in order to test whether the jump trajectories in a vertical plane were modified depending on wind, we recorded the vertical body angle (angle of the jump trajectory in a vertical plane at the beginning of the leap, **Figure 4** in **APPENDIX 3**), and the take-off velocity (velocity after the jump, taking into account only the initial trajectory of the jump without deceleration by gravity; Hill 2006, Nabawy et al. 2018). To determine whether spiders changed the direction of their jumps in the horizontal plane, we also measured the horizontal angle (angle of the cephalothorax on the horizontal plane just before jumping, or the direction the spider 'faced', **Figure 1**), the horizontal displacement (spider position on the starting platform immediately prior to leaping, **Figure 1**), and spider weight. Moreover, to evaluate and compare jump performance between species we also recorded scanning duration (time in which the spider was actively

inspecting its surroundings; scanning phase ended when the spider jumped off the starting platform), fixation duration (a component of scanning; the time in which the motionless spider faced the landing platform prior to jumping; Tarsitano & Jackson 1992, Tarsitano & Andrew 1999), and jump outcome (a successful jump was scored when the spider landed on the landing platform; a failed jump was scored if the spider landed in the water - even if the legs touched the landing platform). For scoring, we used Tracker v. 5.0.7 to measure take-off velocity and vertical body angle, and QuickTime Player with PixelStick v. 2.15.0 to measure horizontal angle and distance displacement variables, as well as jump outcome and fixation duration. Data set from horizontal adjustment, horizontal angle, scanning duration, and fixation duration were obtained from the above view videos. In like manner, vertical body angle and take-off velocity measurements were taken from the side view videos.

All analyses were done with R v. 3.5 (R Development Core Team 2018). To denote if spiders behaved differently as a consequence of treatment, species, or jump outcome, we used linear mixed-effects (LME) models fitted using maximum likelihood methods for Experiment 1. Species and treatment were included as fixed factors, and subjects were specified as the random factor. Model selection was performed by calculating the lowest AIC value (Akaike Information Criteria, Crawley 2007). We used the R packages 'nlme' (Pinheiro et al. 2018) for LME analysis, 'gmodels' for contrast tests (Warnes et al. 2015), and 'ggplot2' (Wickham 2009), 'ggpubr' (Kassambara 2018), and 'cowplot' (Wilke 2017) for graphing.

We performed models to test for effects of horizontal displacement, angle, vertical angle, and take-off velocity as the response variables, and for the vertical body angle, which contained the interaction between species and jump outcome. Scanning duration was log-transformed and the model did not include interactions between response variables. Fixation duration was also log-transformed and the model included the 'treatment:species' interaction. Contrast analyses were also applied to this model for comparisons between treatments within each species.

To determine if the spiders adjusted their horizontal displacement depending on their weight in Experiment 1, we performed a linear regression for each treatment. Additionally, we analysed the probability of jump success according to wind speed (no wind, low wind, and high wind). Here, using the R package 'lme4' (Bates et al. 2015), we compared jump performance as a function of spider species and wind treatment using a generalized linear mixed model (GLMM) with a Laplace approximation. The GLMM used jump outcome as the response variable, species and treatment as fixed factors, and spider identity as the random factor. The model was reduced stepwise by excluding non-significant terms, starting with the least significant interactions (Crawley 2007). The GLMM used a binomial error structure and logit function. Using a final GLMM, we

also investigated whether cognitive attributes (i.e., scanning and fixation duration) affected jump accuracy (jump success) by species.

For Experiment 2, we classified whether the spider jumped during wind or no wind, and jump outcome. As in Experiment 1, we recorded horizontal displacement, horizontal angle, scanning duration, and fixation duration. In addition, we measured the latency to jump as the elapsed time (s) from the beginning of the trial to the jump. To determine if spiders preferred jumping without wind, we used a 2x2 Chi-squared test of independence to compare the number of spiders that jumped with and without wind. Additionally, to determine if jump outcome was related to the wind incidence at the moment of the jump we used a 2x2 Fisher's exact test. Differences in horizontal displacement, horizontal angle, scanning duration log(s), fixation duration log(s), and latency to jump log(s) between wind and no-wind conditions were analysed using t-tests.

Results

Experiment 1

In terms of jump trajectory, for the vertical body angle there was a significant effect of species, with *Portia*'s jumps being about 10º higher than *Trite*'s (**Figure 2**; **Table 1**), but no effect of treatment, while take-off velocity was neither affected by treatment, nor species (**Table 1**).

Regarding the horizontal direction of the jump, the horizontal angle of the cephalothorax at take-off was unaffected by species, but was affected by treatment, being more downwind (Higher than 0º) when spiders encountered wind (high and low) than in control trials (**Figure 3**; **Table 2**). However, horizontal displacement was not affected by species or treatment (**Figure 4**; **Table 2**). Similarly, spider weight did not affect horizontal displacement prior to jumping in control (adjusted $R^2 = 0.042$, $F = 2.47$, $P = 0.126$), low wind (adjusted $R^2 = -8.24^{-03}$, $F = 0.713$, $P = 0.404$), or high wind (adjusted $R^2 = -0.018$, $F = 0.347$, $P = 0.560$) treatments.

There were no differences between species on scanning duration, but spiders scanned for longer in control trials than in high wind trials (**Figure 5A**; **Table 3**). There was an interaction between treatment and species for fixation duration; in *Trite* fixation duration did not differ between treatments, but in *Portia* it was shorter in high wind trials compared with control trials (**Figure 5B**; **Table 3**).

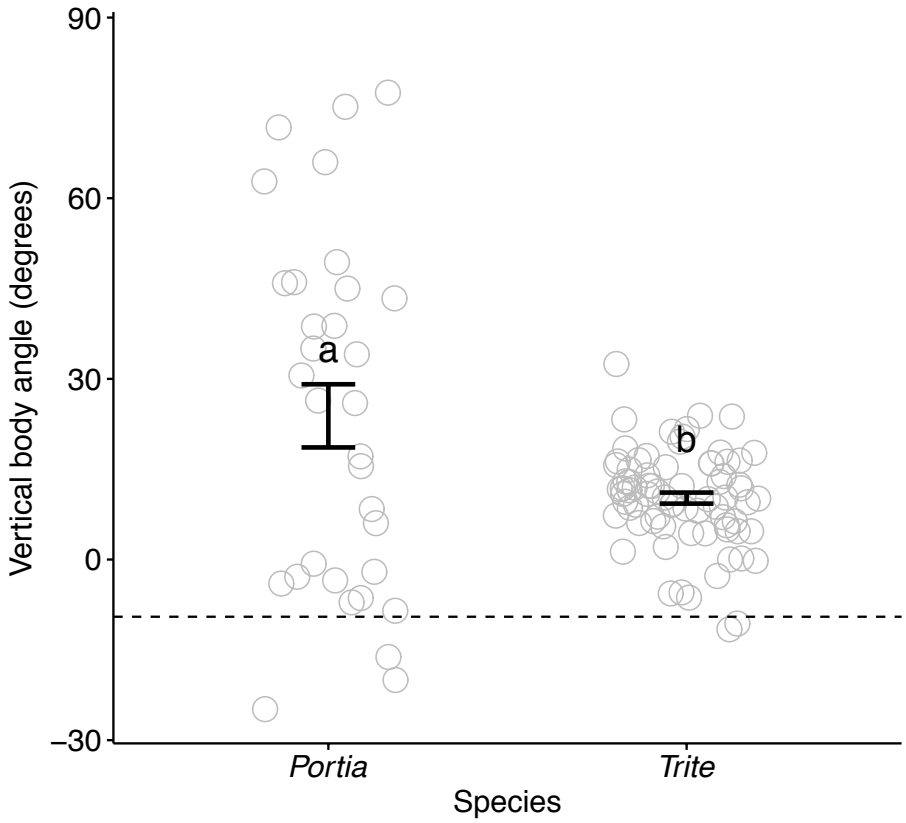


Figure 2. Mean (±SEM) effect of species on the vertical angle of the body before the jump. Letters denote significant differences between groups. Dotted line depicts a straight line from the starting platform to the landing platform.

Table 1. Summary of the Linear Mixed Effect Models for the vertical body angle, and for take-off velocity. The models had spider ID as the random factor and accounted for species and treatment as fixed factors. CI = confidence interval at 95%.

Variable	**Estimate**	**CI**	**DF**	**t**	***P***
Model: Vertical body angle					
Intercept	22.823	14.024 – 31.631	68	5.076	<0.0001
Treatment [High]	2.310	-4.412 – 9.034	68	0.672	0.503
Treatment [Low]	-0.706	-7.360 – 5.947	68	-0.207	0.836
Species [*Trite*]	-13.253	-22.789 – 3.718	35	2.768	0.009
Model: Take-off velocity					
Intercept	64.957	58.417 – 71.495	68	19.448	<0.0001
Treatment [High]	4.867	-0.684 – 10.419	68	1.716	0.090
Treatment [Low]	4.669	-0.829 – 10.167	68	1.662	0.101
Species [*Trite*]	-5.836	-12.697 – 1.024	35	-1.694	0.099

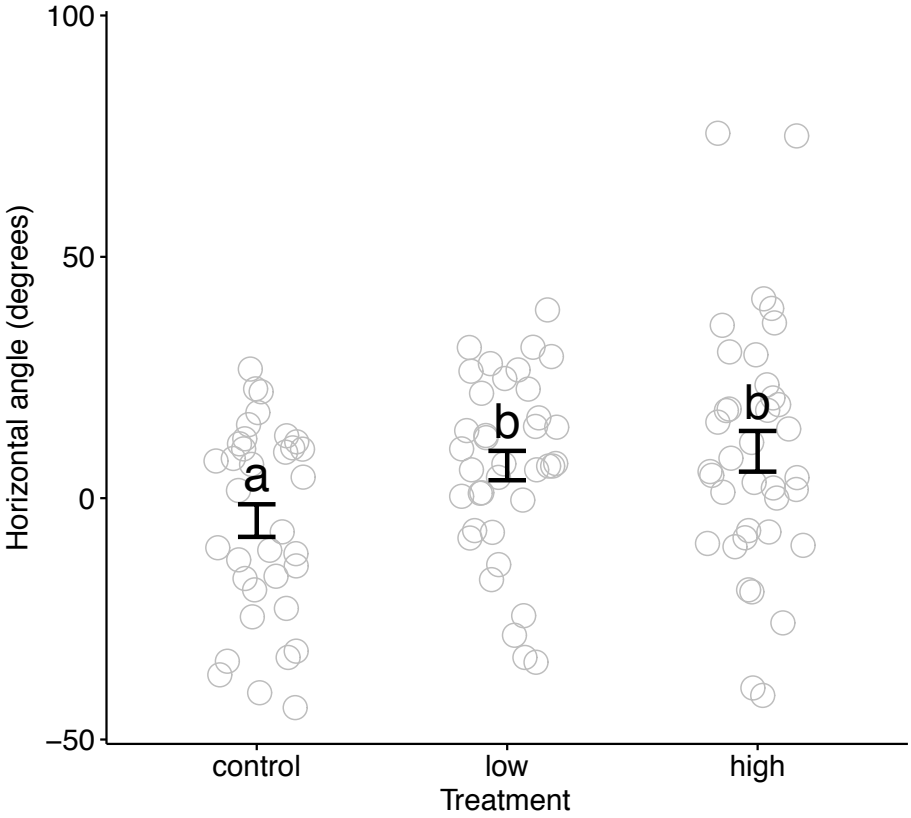


Figure 3. Mean (±SEM) effects on the horizontal angle of the cephalothorax by wind treatment. Letters denote significant differences among groups. On the y-axis 0^{o} represents a right-angle jump with respect to the edge of the starting platform; negative values represent upwind jumps and positive values depict downwind jumps.

Table 2. Summary of the Linear Mixed Effect Models for horizontal displacement and for horizontal angle of cephalothorax. Models had spider ID as the random factor and accounted for species and treatment as fixed factors. Interactions between fixed factors were not accounted for. CI = confidence interval at 95%.

Variable	**Estimate**	**CI**	**DF**	**t**	***P***
Model: Horizontal displacement of body					
Intercept	-0.771	-2.006 – 0.463	70	-1.223	0.225
Treatment [High]	-0.783	-1.939 – 0.372	70	-1.327	0.188
Treatment [Low]	-0.880	-2.033 – 0.272	70	-1.494	0.139
Species [*Trite*]	1.006	-0.234 – 2.247	35	1.616	0.115
Model: Horizontal angle of cephalothorax					
Intercept	-2.731	-12.686 – 7.223	70	-0.537	0.592
Treatment [High]	14.243	4.672 – 23.815	70	2.912	0.004
Treatment [Low]	11.289	1.738 – 20.840	70	2.313	0.023
Species [*Trite*]	-2.561	-12.439 – 7.316	335	-0.516	0.608
Contrast test for Horizontal angle of cephalothorax					
Low wind *vs* High wind	-2.954	-12.575 – 6.667	-0.614	70	0.541

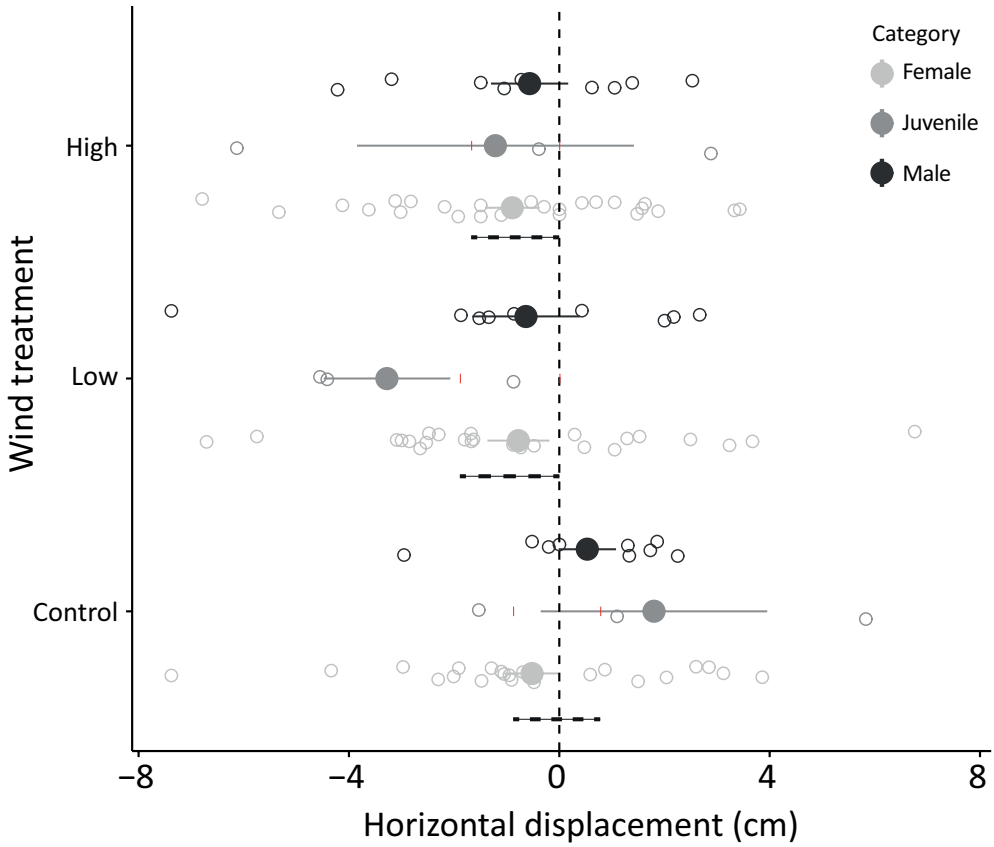


Figure 4. Horizontal displacement of spiders (by category) prior to jumping when exposed to different wind treatments. Data are presented such that the wind direction is depicted from left to right. Note the slight upwind displacement of the standard errors (solid lines), from control compared to wind trials (low and high wind). Dashed lines below each treatment: Overall SEM for all spiders per treatment.

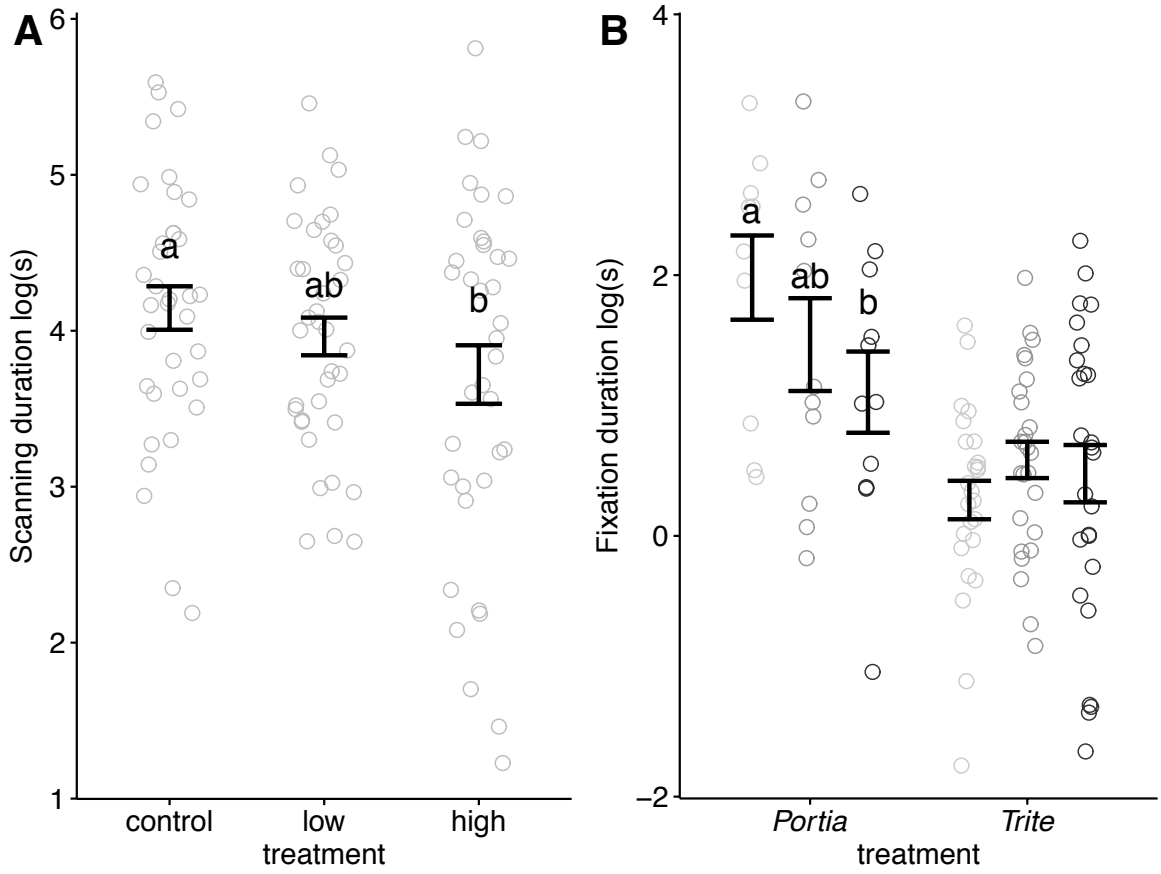


Figure 5. Mean (±SEM) effect of A) wind treatment on scanning duration and B) fixation duration by species (control = light grey, low wind = dark grey, high wind = black). Letters denote significant differences between groups.

Table 3. Summary of the Linear Mixed Effect Models for scanning duration and fixation duration. Models had spider ID as the random factor and accounted for species, treatment and jump outcome as fixed factors for the scanning duration model, as well as the interaction between species for the fixation duration model. CI = confidence interval at 95%.

Variable	Estimate	CI	DF	t	*P*
Model: Scanning duration, log(s)					
Intercept	52.961	34.686 – 80.866	70	18.359	<0.0001
Treatment [High]	0.656	0.440 – 0.979	70	-2.058	0.043
Treatment [Low]	0.836	0.561 – 1.247	70	-0.875	0.384
Species [*Trite*]	1.278	0.837 – 1.952	35	1.155	0.255
Contrast test for Scanning duration, log(s)					
Low wind *vs* High wind	1.274	0.242 – 1.904	70	1.204	0.232
Model: Fixation duration, log(s)					
Intercept	7.109	4 – 12.638	68	6.614	<0.0001
Treatment [High]	0.441	0.211 – 0.921	68	-2.156	0.034
Treatment [Low]	0.609	0.294 – 1.261	68	1.319	0.191
Species [*Trite*]	0.186	0.093 – 0.372	35	-4.783	<0.0001
Treatment [High]*:* Species [*Trite*]	2.754	1.153 – 6.577	68	2.257	0.027
Treatment [Low]*:* Species [*Trite*]	2.214	0.934 – 5.247	68	1.787	0.078
Specific comparisons for Fixation duration, log(s) in *Portia fimbriata*					
Control vs Low wind	1.639	0.775 – 3.468	67	1.319	0.191
Control *vs* High wind	2.266	1.061 – 4.839	67	2.156	0.034
Specific comparisons for Fixation duration, log(s) in *Trite planiceps*					
Control vs Low wind	0.740	0.458 – 1.196	67	-1.253	0.214
Control *vs* High wind	0.822	0.509 – 1.329	67	-0.813	0.418

The probability to perform a successful jump was affected by both treatment and species (**Table 4**), with more jumps being successful in control trials than in low and high wind trials. Similarly, proportion of successful jumps in low wind trials was marginally higher than in high wind trials. Additionally, the proportion of successful jumps was significantly lower ($P = 0.004$, Fisher exact test) in *Portia* (19/32 successful jumps) than in *Trite* (67/77). In terms of how potential cognitive attributes impacted jump success, we found that both in *Trite*, and especially in *Portia*,

spiders that scanned for longer had significantly better jump accuracy, although fixation duration had no effect (**Figure 6**; **Table 4**).

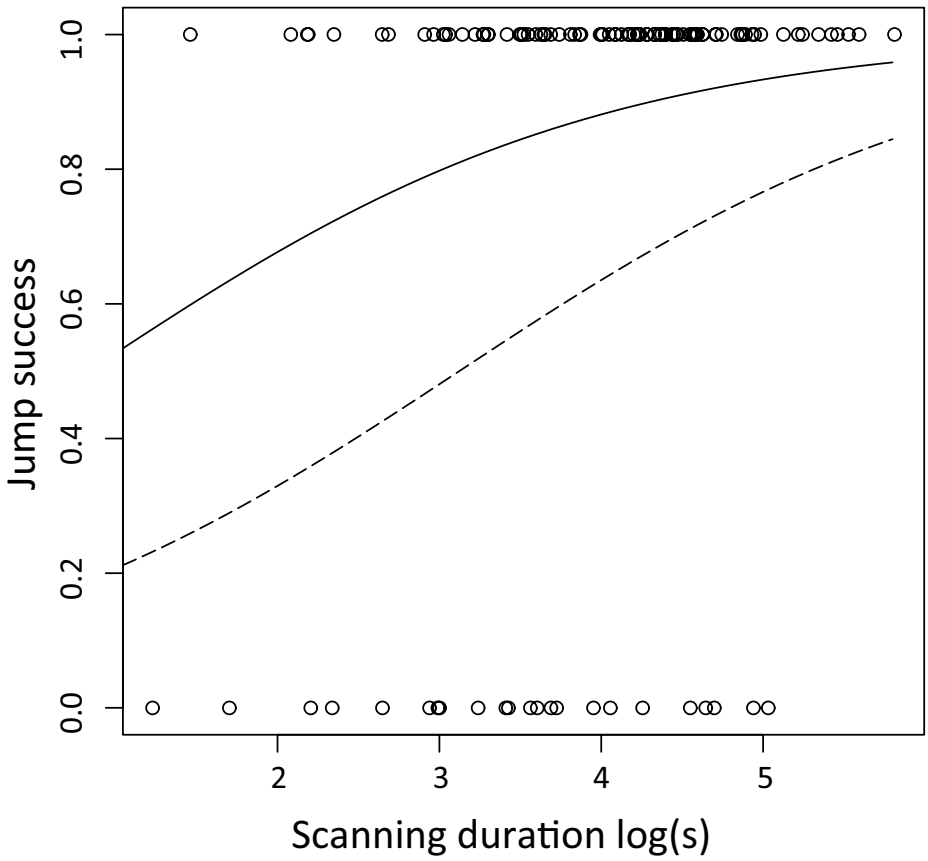


Figure 6. Effect of scanning duration on jump success in *Portia* (dashed line) and in *Trite* (solid line) jumping spiders.

Table 4. GLMM outputs indicating effects of species and treatment on jump outcome (top) and effects of species, scanning duration, and fixation duration on jump outcome (bottom). N = 37, n = 109. CI = confidence interval at 95%.

Variable	Estimate	CI	Z	*P*
Model: Species and treatment effects on jump outcome				
Intercept	2.348	0.357 – 6.182	1.935	0.053
Treatment [High]	-2.422	-5.107 – -0.627	-2.275	0.022
Treatment [Low]	-2.013	-4.577 – -0.231	-1.940	0.052
Species [*Trite*]	2.598	0.568 – 6.469	2.109	0.035
Contrast test				
Low *vs* High	1.155	0.063 – 2.574	1.914	0.055
Model: Scanning and fixation duration on jump outcome				
Intercept	-1.637	-4.998 – 1.546	-1.048	0.295
Species [*Trite*]	1.491	-0.470 – 4.050	1.490	0.136
Scanning duration (log)	0.931	0.168 - 1.974	2.183	0.029
Fixation duration (log)	-0.646	-2.050 – 0.420	-1.108	0.268

Experiment 2

The number of individuals that jumped with wind (n = 11) was significantly lower (χ^2 = 4.828, df = 1, P = 0.028) than the number that jumped without wind (n = 24). However, there was no relationship between the presence/absence of wind at the time of the jump and jump outcome (confidence interval = 0.005 to 37.511, odds ratio = 0.446, P = 0.536). We also found no significant differences in horizontal displacement (t = 1.142, df = 19.386, P = 0.267), horizontal angle (t = 0.298, df = 31.028, P = 0.767), scanning duration (t = -0.134, df = 21.178, P = 0.894), fixation duration (t = -1.286, df = 20.164, P = 0.212), or latency to jump (t = -0.775, df = 21.264, P = 0.446) between jumps with and without wind.

Discussion

Ballooning crab spiders (Thomisidae) have an awareness of wind direction (Cho et al. 2018). Salticids also exhibit ballooning behaviour (Horner 1975), and, unlike crab spiders, jump for locomotion and for hunting. Considering this, we predicted that salticids would adjust their

jumps to account not only for the presence of wind, but also its direction and speed. We found that, in intermittent wind conditions, salticids preferred to jump without wind. Additionally, we found differences in the direction in which spiders faced (horizontal angle of the cephalothorax) prior to jumping. Without wind, spiders faced the landing platform directly, positioning their body axis perpendicular to the starting platform's edge, yet when exposed to wind, they positioned the body axis downwind, such that the jump was favoured by the wind's force. While still somewhat inconclusive, as differences in jump trajectories depending on the strength of the wind were subtle, we believe that, overall, our results support the notion that salticids account for wind conditions at the time of jumping. However, our results are also consistent with the idea that, especially among *Portia*, wind decreases the decision-time before jumping, resulting in poor jump accuracy, suggesting a trade-off between careful decision-making and time.

A non-significant tendency to move marginally closer to the wind tunnel in the presence of wind was observed in the horizontal displacement of the body. We suggest that the relative lack of change in horizontal displacement may account for jump success being higher in trials without wind, and being higher in low wind compared with high wind. However, jump success across both species, even in high wind, was significantly higher than chance levels (26/37, $P = 0.02$, binomial test), suggesting that other adjustments contribute to jump success in windy conditions.

The combination of vertical body angle and take-off velocity were used as an indicator of the jump trajectory setup by the spider. We expected steeper upward trajectories in control trials and flatter, more direct, trajectories with high wind trials. However, spiders did not seem to significantly adjust their take-off characteristics (vertical angle, take-off velocity) according to wind incidence or wind speed. Thus, adjustments may depend more on the distance of the landing area than on wind. *Phidippus regius* adjusts its trajectory and take-off speed based on the location of the landing point, being slower and flatter when the landing platform is close (2 x body length gap: take-off velocity = 62.5 ± 2.5 cm^{s-1}, vertical angle = 15 ± 5°) and being faster and steeper for longer gaps (e.g., 4 x body length gap in a level jump: 92.5 ± 2.5 cm^{s-1}, 25 ± 5°; Nabawy et al. 2018). Our gap distance was about 2.5 body lengths and we observed slow, flat, jumps in both species (*Portia*: 68.3 ± 2.7 cm^{s-1}, 7.5 ± 4°; *Trite*: 62.4 ± 1.5cm^{s-1}, 9.9 ± 0.8°). Our results are consistent with the suggestion that a more direct trajectory ensures focus on the landing point before jumping, whereas if the spider uses steeper jumps requiring higher take-off velocities, precision is compromised, as sight is lost due to the upwards tilt of the cephalothorax (Nabawy et al. 2018). Nevertheless, we did observe marked differences in jump precision between species.

We anticipated that *Portia* would outperform *Trite* in terms of jump success. Descriptive studies have shown exceptional spatial abilities among *Portia* (Jackson & Blest 1982, Jackson &

Hallas 1986b, Jackson & Wilcox 1993), and comparative studies have re-affirmed *Portia*'s overachievement within the Salticidae. Specifically, *Portia* has better route assessment (Tarsitano & Jackson 1997, Cross & Jackson 2016), visual discrimination (Tarsitano & Jackson 1992, 1994, Jackson & Tarsitano 1993), and improvisation of novel shortcuts (Aguilar-Argüello et al. 2019a) than *Trite*. In this study, however, by having significantly higher proportion of successful jumps, *Trite* seems to be a more skilful jumper than *Portia,* whose overall proportion of successful jumps was no greater than chance, indicating that *Portia* struggled to perform the task. A factor that could explain *Portia*'s unexpectedly poor performance is that, being laboratory-reared, the individuals tested had not been in contact with wind, whereas *Trite* were field-collected, suggesting that experience with wind may be important in assessing the jump. Further research comparing the capability of lab-reared and field-collected *Trite* would be instructive in assessing the role of learning in sensory perception. Nevertheless, despite being lab-reared, in our previous work on spatial ability, *Portia* has outperformed *Trite* (Aguilar-Arguello et al. 2019, 2020). Instead, our results, in which *Portia*'s jump accuracy significantly improved with long scanning duration before jumping, suggest instead that windy conditions were stressful, resulting in decreased scanning time and concomitant jump failures. This effect was much more pronounced in *Portia* than in *Trite*, possibly due to differences in the habitat in which each species is found.

Interspecific differences in jump success in windy conditions may be due to the capabilities of the animal to accurately gauge wind. Previous work has demonstrated that *Portia fimbriata* is able to perceive wind during predation, but its performance in using wind in its favour to mask an approach towards prey is low compared to other spartaeines (Cerveira et al. 2003). *Trite* may be more sensitive to – or less stressed by – wind than *Portia,* allowing it to more accurately assess the jump. The habitat structure of these species differs greatly: *Portia* inhabits tropical forests with dense vegetation (Jackson & Hallas 1986a) in which windy conditions may be negligible compared to the flax vegetation dominant in *Trite*'s habitat (Forster 1979), which is shorter and often close to wetlands in which windy conditions are frequent (Singers & Rogers 2014). Additionally, as they spend most of the time in dark environments inside rolled-up flax leaves, *Trite* may rely more heavily on cues other than vision compared to most salticids. Previous studies on *Trite* indicate the use of vibratory signals for courting (Taylor & Jackson 1999), use of airflow disruptions for catching prey (Forster 1982), and navigation in darkness (Taylor 1995). A morphological study comparing the trichobothria of *Portia* and *Trite* may elucidate differences between species.

Our results suggest that wind tends to accelerate the decision-making process of jumping. During visual scanning, salticids systematically move their cephalothorax and body to inspect their surroundings using their AME. This is believed to be associated with decision-making processes

(Tarsitano & Andrew 1999, Cross & Jackson 2016). In contrast to previous work, where *Portia* scanned for longer than *Trite* (Aguilar-Arguello et al. 2019, 2020), here there were no differences in scanning duration between species. Nevertheless, spiders scanned for longer in control conditions compared to high wind, suggesting that wind may accelerate decision-making. The fact that spiders that scanned for shorter periods had poorer jump accuracy suggests that this decision-making process is subject to trade-offs. We also measured fixation duration (i.e., gaze) just before jumping, as this, like scanning duration, may provide an indication of the difficulty of the assessment task (e.g., Cerveira et al. 2019). *Portia* had longer fixation durations during control trials than in high wind, whereas *Trite* did not exhibit differences in fixation duration between treatments. Overall, our results suggest that, at least in *Portia*, wind speeds up decision-making regarding jumps, and this is reflected in *Portia*'s reduced jump accuracy with increasing wind speed. Nevertheless, interpretations regarding the high wind treatment should be taken cautiously, as we do not know if the spider's faster scanning and fixation times are attributed to wind speed, the noise of the leaf blower, or a combination of both: scanning duration was not affected by noise, but fixation duration was shorter with the presence of noise (**APPENDIX 3.1**). Notably, the lack of change in *Trite*'s fixation duration is reflected in previous work, in which we have consistently found that *Trite*'s decisions about jumping in risky situations are quicker than *Portia*'s (Aguilar-Arguello et al. 2019), apparently at no cost to jump precision, unlike in *Portia*.

Our final prediction, that spiders would tend to jump in the absence, rather than in the presence, of wind, was confirmed. These results support the idea that salticids are aware of windy conditions, as suggested in previous work on *Portia*'s smokescreening behaviour. When invading their webs, *Portia* is more likely to approach the target prey spider during 30 s cycles of wind presence than during 90 s cycles without wind (Wilcox et al. 1996, Cerveira et al. 2003), whereas here, we expected spiders to jump without wind to save energy and avoid risk.

In summary, our findings suggest that spiders can assess wind and behave in an optimized manner depending on context, attending to information within short (here, 10 s) cycles, and adjusting their jump trajectories and decision-making scanning behaviour based on conditions. However, wind may be a stressor that causes a trade-off between time to make a decision and good decision-making in salticid spiders.

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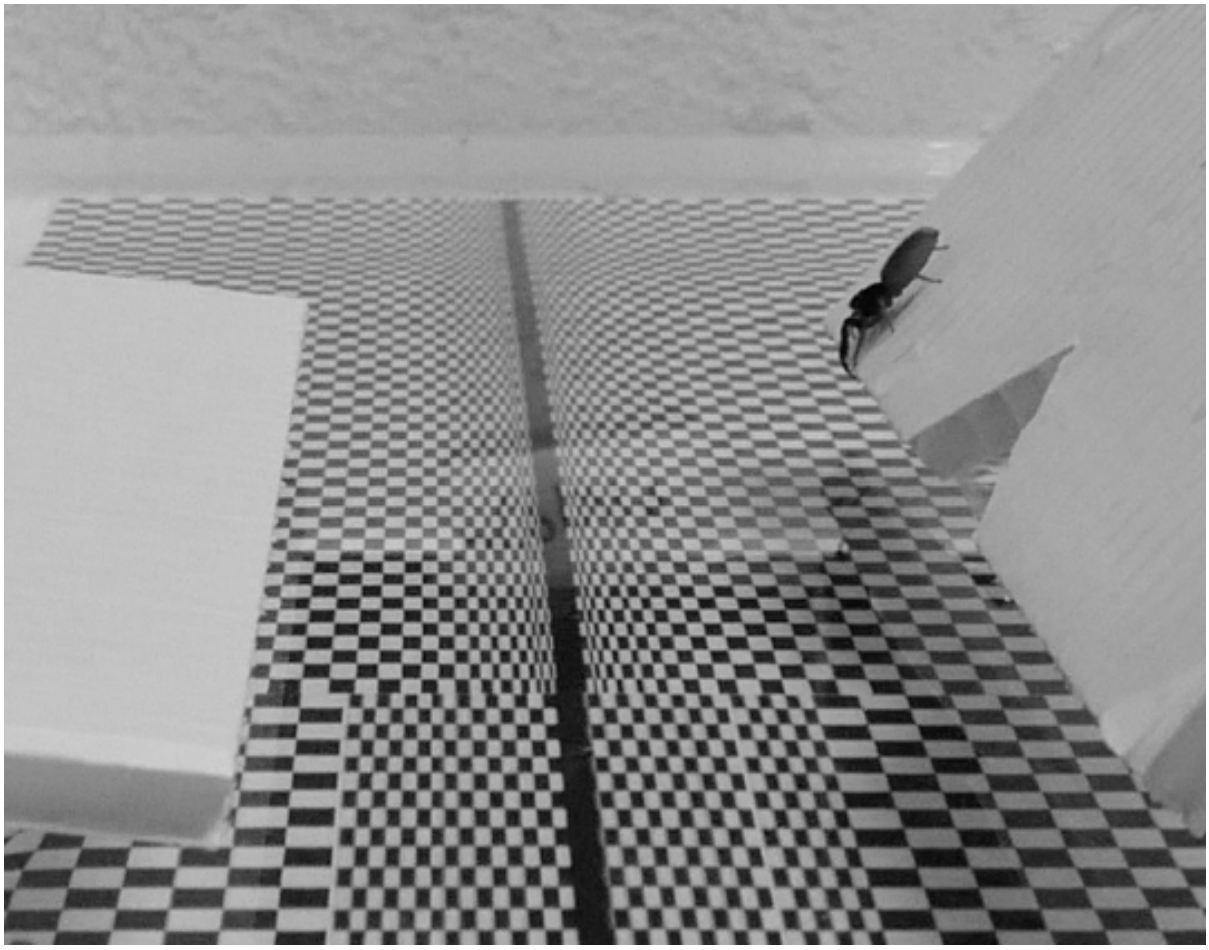
CHAPTER FIVE. Texture as a monocular depth perception cue in jumping spiders



Decision-making in *Trite planiceps*, before jumping to the landing platform in Experiment 1.

Abstract

The usefulness of vision is such that many animal taxa have independently evolved eyes. Research using optical illusions in non-human animals with different types of eyes has demonstrated that these can share characteristics to our own visual processes. In experiments with and without optical illusions, we evaluated depth perception in the jumping spider (Salticidae) *Trite planiceps* by the use of 'texture density' (depth estimation through surface texture comparisons, with greater distances having larger differences in the density of the texture). Salticids use exceptional vision to actively stalk and leap on prey, and to find mates. They have four pairs of eyes, two of which (anterior lateral and anterior medial) are forward-facing, but - in principal - stereopsis could only be mediated by the former. In Experiment 1, *Trite planiceps* showed no preference to jump over an illusion resembling a trench over a no-illusion control pattern. In visual cliff experiments, spiders tended to choose the area with a false 'low drop' over a false 'high drop' with same texture densities, but showed no preference for either area when presented with substrates with different texture densities at a constant height. Finally, we selectively occluded either both anterior lateral and one anterior medial eye (monocular treatment), both anterior lateral eyes (binocular treatment) or none (control), and induced spiders to jump over a 50 mm gap with two different physical drops. Neither control spiders, nor spiders with only binocular cues from the anterior medial eyes, exhibited a height preference, whereas spiders with monocular vision preferred to jump over the low drop gap. Results suggest that *T. planiceps*, although not fooled by the trench illusion, does use texture density as a depth perception cue.

Introduction

For many animals, vision is paramount for awareness of their surroundings, as it provides information about danger, features of objects, and whether something is edible or a potential mate. The properties of vision, in that objects are easily localisable (when visible) and information is up-to-date, are of sufficient selective importance that evolution has given rise to multiple independent instances of image-forming structures (eyes) that enable visually-guided behaviour in a multitude of taxa (Halder et al. 1995, Gehring 2002, Smith 2008, Nilsson 2013). Of the three main types of eyes that have evolved (camera-type, compound, and mirror eyes), two are specialised for high spatial acuity vision, enabling good visual detail of objects to be discerned. These are the camera-type eyes found among modern arachnids, cephalopods and vertebrates, which consist of a lens that projects onto a retina, and, to a lesser extent, the compound eyes of insects, which consist of

multiple independent lenses (or ommatidia) which create a single, somewhat 'pixelated', image (Land 1985a, Nilsson 2013).

Physiological, molecular and morphological studies have significantly contributed to our understanding of the perception of different organisms, yet behavioural experiments are crucial to fathom out eye function and visual perception, such as colour (Neumeyer 1981, 2012, Williams 1974) and depth (Ashida 1972, Kral 1998, Josef et al. 2014). Additionally, while there is detailed information about how light is processed by photoreceptors, many questions remain regarding subsequent levels of processing by the nervous system (Kelley & Kelley 2014), and studies using optical illusions are particularly useful to understand visual perception and processing.

Visual illusions work because the visual system makes assumptions about the elements of the illusion as a consequence of previous experience and cognitive processing (Josef et al. 2014). This leads to a misinterpretation of reality, either by seeing something that it is not, in fact, present (e.g., Kanisza figures; Hermann grid illusion) or through the illusion of movement on a static target (e.g., waterfall illusion). Like humans, other animals are deceived by optical illusions: bottlenose dolphins, chickens, pigeons, and at least some fish are deceived to greater or lesser extents by the Ebbinghaus illusion (Nakamura et al. 2008, Murayama et al. 2012, Rosa Salva et al. 2013, Sovrano et al. 2015), while pigeons, parrots and macaques are deceived by the Müller-Lyer illusion (Nakamura et al. 2006, Pepperberg et al. 2008, Tudusciuc & Nieder 2010). Similarly, bees, cuttlefish, cats, monkeys, owls, and fish are susceptible to the illusory contours of Kanizsa figures (van Hateren et al. 1990, Nieder 2002, Zylinski et al. 2012, Agrillo et al. 2013, Fuss et al. 2014), suggesting that visual processing and perception in these animals, some of them with different types of eyes, may share characteristics to our own. This is further suggested by a study showing that cuttlefish are also deceived by a 2D optical illusion based on the concept of 'texture density gradient', where an image can provide the illusion of depth through a graded decrease in the size of the elements on a surface (Gibson et al. 1955, Frisby & Stone 2010).

A related paradigm that has helped understand vision-based depth perception is the 'visual cliff experiment', which consists of exposing an animal to false low and high vertical drops with visual textures on the substrate (Walk & Gibson 1961). Using monocular cues, animals can estimate different heights by comparing the density of the texture of two presented surfaces, such that the density difference can be used to estimate the relative distance to each surface (Gibson 1950). As many animals are instinctively averse to sudden large drops, this method allows avoidance behaviour to be easily quantified across a wide variety of vertebrates, including humans (Walk & Gibson 1961, Schwartz et al. 1973, Richards & Rader 1983). A modification of the visual cliff experiment, using optical illusions, was recently tested in cuttlefish (Josef et al. 2014). Josef et

al.'s (2014) work suggest that there is considerable scope to test how texture density gradients are processed by invertebrates with structurally and physiologically different visual systems and apparently 'simpler' brains, providing the impetus behind this study.

In addition to using differences in texture density, relative depth perception can be achieved by other monocular depth cues. These include size (larger objects are perceived to be closer to the observer than smaller objects), occlusion (objects that partially block another object are perceived as being closer), shadows, and linear perspective (parallel receding lines converge into the horizon) (Frisby & Stone 2010, Lazareva 2017).

Absolute depth perception cues provide precise assessment of distance of an object. Instances of this which can be achieved with one eye include accommodation (Harkness 1977, Wagner & Schaeffel 1991), where the lens changes shape to focus on specific objects at different depths, and motion parallax, in which an animal performs head movements which enable distance estimation by the relative motion of the object compared to the motion of other objects located closer or farther away (Kral 2006). Other absolute depth perception mechanisms require two eyes that have overlapping fields of view, such as stereopsis, in which the two disparate images from the two retinae are compared. A second binocular mechanism is convergence, which is the lateral movement of the eyes when focusing on one object. Here, the amount of movement of the eyes towards the centre provides the brain with information about the object's distance (Lazareva 2017).

Jumping spiders (Salticidae) have camera-type eyes that are structurally different from those of vertebrates (Land 1985a), yet provide visual detail rarely matched by any other animal. Indeed, Michael Land (1969a) stated that "jumping spiders are among the most vision-dependent animals". Salticids represent an excellent group in which to test responses to optical illusions relating to depth cues. While moving through the complex three-dimensional habitats that they typically inhabit, it is not uncommon for salticids to encounter gaps in vegetation in which an accurate jump is needed (or a long drop ensues), and it is known that they accurately assess the distance of the landing point based on vision (Nabawy et al. 2018).

Vision in salticids is achieved by three pairs of secondary eyes and one forward-facing pair of primary, or anterior medial, eyes (AME). The AME support colour vision and have outstanding spatial acuity (resolution) (Williams & McIntyre 1980, Nelson & Jackson 2012, Zurek et al. 2015). Despite typically measuring less than 500 microns, spatial acuity in the AME can be as high as 0.04^{o}, allowing the individuals to see objects 0.12 mm apart at a distance of 200 mm (Land 1969a, Williams & McIntyre 1980, Nelson & Jackson 2012). A curious anatomical characteristic of the AME is the layered structure of their retinae (Land 1969a). Here, the receptors are arranged in

four tiers, each of which lies on a different focal plane. Because of chromatic aberration due to differential refraction of wavelengths when light enters the cornea, different wavelengths are focused on different layers of the retina, so by comparing how 'in-focus' information is on one tier compared to another, animals may be able to make depth judgements. This has led to the suggestion that salticids use monocular vision based on 'image-defocus', which works by comparing how out-of-focus two or more images are with respect to each other (i.e., comparing the level of defocus of images formed in two photoreceptor layers of the AME; Nagata et al. 2012, Guo et al. 2019). However, among the secondary eyes, which are arranged around the side of the cephalothorax and provide 360° monochromatic vision, one pair, the anterior lateral eyes (ALE), is forward-facing and provides a large region (c. 30°) of binocular overlap, leading to the speculation that this region mediates depth perception in salticids (Land 1985b), and may be used for stereopsis. However, despite there being a number of physiological studies on spider vision, depth perception studies are still scarce and somewhat inconclusive.

Here, our primary objective was to investigate whether the visual system of salticids processes textural information similarly to how we do. Specifically, we wanted to determine if salticids can perceive depth by using the texture density of the substrate with and without optical illusions. We first adapted the methodology used on cuttlefish by Josef et al. (2014) to test if salticids are fooled by an optical illusion that resembles a deep trench in the bottom of a pool, and if they avoid jumping over this visual pattern. We also explored salticid behaviour in a visual cliff experiment, predicting that spiders would tend to avoid the area with the high drop. We then isolated the texture density as the only monocular depth perception cue by modifying the visual cliff experiment, predicting that spiders would tend to avoid the ground with a texture suggestive of a high drop. In a final experiment, we ruled out binocular mechanisms provided by the ALE through sequential occlusion of these eyes. Here, our prediction was that spiders would perform similarly with and without binocular cues provided by the ALE, as it is possible that salticids may heavily rely on a monocular depth perception mechanism (e.g., Nagata et al. 2012). We did not occlude both AME in these experiments because there is considerable evidence that salticids rarely perform directed movements – let alone jumps – when these eyes are covered (Ximena Nelson, pers. comm. on unpublished data; Zurek et al. 2010).

Methods

Trite planiceps Simon is a large (6–13 mm) salticid endemic to New Zealand and is typically found in coastal areas where it inhabits the rolled-up flax leaves of *Phormium tenax* and *Cordyline* spp. (Forster 1979). *Trite* were field-collected in Christchurch, and were transferred to the

laboratory, where they were housed individually in 1 L transparent plastic containers. Rearing conditions were similar as performed in previous studies (Aguilar-Arguello et al. 2019, **Chapter 3**).

Experiment 1. Texture gradient optical illusion

The arena consisted of a plastic container (530 x 400 x 60 mm) filled to a depth of 35 mm with water (i.e., the pool) containing two plastic platforms (50 mm wide x 150 mm long). The pool was surrounded by four identical high-resolution pictures of foliage, providing motivation for the spiders to exit the pool and obstructing external visual stimuli, as in previous studies (Aguilar-Arguello et al. 2019, **Chapter 3**).

The starting platform was inclined 45° towards the landing platform and the lowest part of the starting platform was 5 mm above the water level, as was the landing platform (**Figure 1**). The task consisted of spiders jumping across the 50 mm gap between the platforms, which they were motivated to do to attempt to exit the pool. While this is not an exceptionally long jump, it is longer than the 20 - 30 mm jumps that they typically make and it was over water, to which salticids are very averse and should increase perceived risk (Aguilar-Arguello et al. 2019). On the base of the pool, between the platforms, we placed two visual patterns: 1) the treatment, a black and white texture which provides the illusion of a trench and 2) the control, which consisted of a similar optical pattern, based on that used by Josef et al. (2014), which contained no trench illusion (**Figure 2A,B**). Both patterns (230 x 120 mm) were printed on paper, laminated with a matte finish, and glued to a thin aluminium sheet. Each pattern covered one half of the area between the platforms, and the position of each was randomised between trials. Additionally, the position of the whole pool was changed randomly (left configuration, and right configuration) to control for behaviour based on external cues. Finally, to prevent spiders jumping from the middle of the starting platform (i.e., across the area where the two patterns joined together), and to reduce the chances of spiders making diagonal jumps, a triangular portion (25 x 25 x 35 mm wide) was cut out of the front edge of the starting platform.

For this experiment, we tested 29 spiders (16 females, 4 males, and 9 adults). Trials ended once the spider jumped from the starting platform to the landing platform, or whenever 30 mins had elapsed without a jump. Trials were considered successful only when the individual oriented towards the visual treatment, and when the spider jumped to the landing platform. When there was an unsuccessful trial, the spider was tested on another day. Each spider was only given one successful trial.

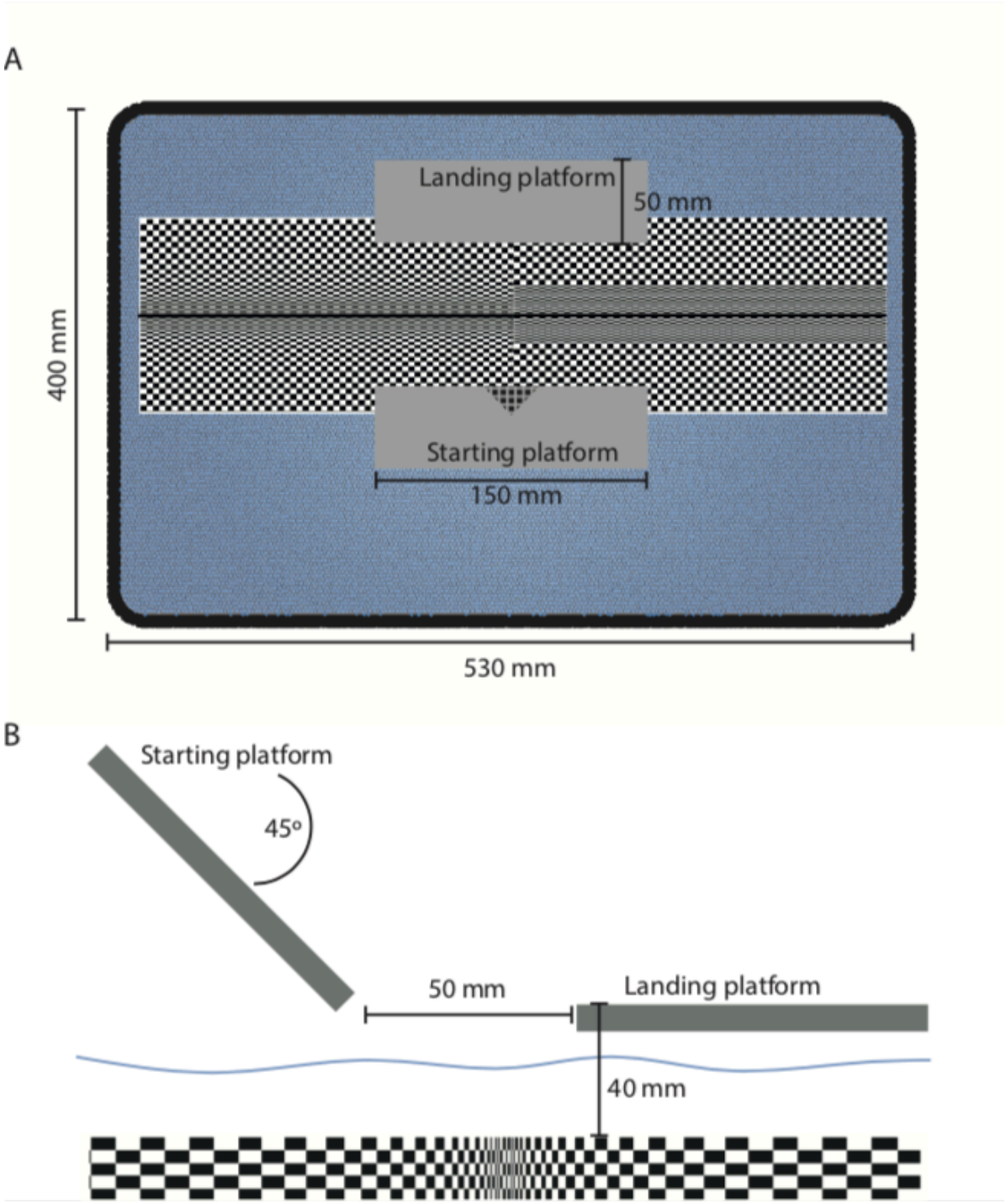


Figure 1. Test arena for Experiment 1. (**A**) Top view of the pool, treatment on the left and control on the right. (**B**) Side view of the pool. The inclination of the starting platform allows a direct view of the 'trench'.

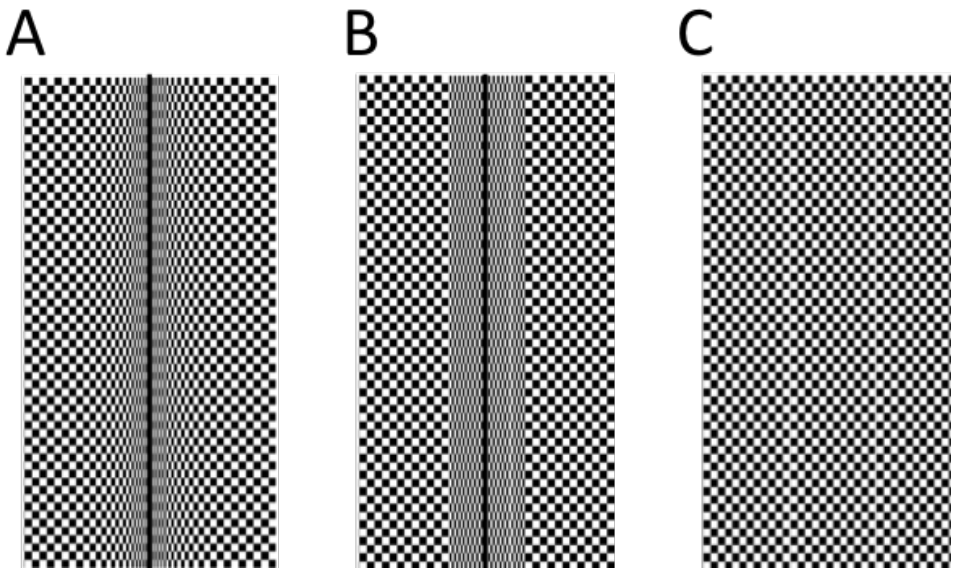


Figure 2. Texture patterns used in experiments. (**A**) Optical Illusion (treatment) used in Experiment 1: gradual texture with a false-depth element in the shape of a deep trench (based on Josef et al. 2014). (**B**) Control texture used in Experiment 1: a non-gradual pattern with spatial elements similar to those in pattern A, but lacking the continuous size gradient that creates the illusion of depth. (**C**) Visual pattern used in both depths in Experiments 2 and 4: a uniform checkerboard pattern.

Trials were recorded simultaneously with a Logitech c 920 HD Pro webcam from above and with a Panasonic LUMIX TZ90 digital camera from the side. From video, we recorded jump choice (if the spider jumped over the treatment or the control pattern), and the number of random jumps (n jumps towards any part of the pool other than towards the landing platform). From the latter, we also recorded the number of jumps towards each visual pattern (i.e., how many of the random jumps were directed toward the treatment or control, as if the spider aimed to land on them). We also recorded the latency to jump (s) from the start of the trial.

To determine if spiders preferred to jump over one of the two patterns, we used a Chi-squared test of independence to compare the number of individuals that jumped over the control with the number of individuals that jumped over the treatment. We also performed a survival analysis to compare the probability to jump over the treatment and control patterns in relation to time. Specifically, we used Accelerated Failure Time models (AFT) with a lognormal distribution (Fox 2001) with latency to jump as the response variable and jump choice as the independent variable. The AFT model was selected based on the distribution with the minimum AIC value, which exhibited the best fit to the data (Cox 1972). Finally, to determine if spiders had a tendency

to jump towards a particular pattern, we used a Wilcoxon matched-pairs signed rank test to compare the number of random jumps for the trench and for control patterns.

Experiment 2. Visual cliff experiment

The arena consisted of a glass sheet (190 x 190 mm) suspended 435 mm from the ground using retort stands. This sheet was divided in half by a 'runway' (a plastic platform 5 mm high x 25 mm wide), with the entire arena being covered by a glass bowl (100 mm high x 180 mm diameter) smeared with petroleum jelly to prevent the spiders from climbing its walls.

A 'low drop' area (95 mm x 190 mm) was suspended 35 mm below the sheet of glass, encompassing half of the area of the sheet. The 'high drop' area consisted of the ground of the arena (510 x 540 mm), and was visible from the other half of the glass sheet. Therefore, spiders placed on the runway could choose between jumping or walking towards the low drop, with a 40 mm relative height change, or the high drop, with a 440 mm relative height change (**Figure 3A,B**). The low drop and high drop substrates consisted of a black and white textured checkerboard pattern which had identical squares (5 x 5 mm; **Figure 2C**). Consequently, from the high drop, each square subtended 7.15°, whereas from the low drop each square subtended 0.65°. These are within the limits of spatial acuity of salticid primary eyes, which vary from about 0.17 to 0.04° (Land 1985a, Williams and McIntyre 1980).

In order to control for light conditions for both drops, we used ceiling lighting and a Nikon fibre optic light source to counteract the lack of illumination at the base of the arena. The resulting luminance conditions, as measured at the bottom of the low drop were 440 lux, and at the base of the high drop were 411 lux. Cooking paper was used to cover both light sources to diffuse the light.

We tested 34 spiders (11 females, 5 males, and 18 subadults). Trials started by positioning the spider on the runway and enclosing the arena with the glass bowl. Trial duration was 5 min after the spider jumped or walked off the runway. After each trial, the entire arena was wiped with ethanol to avoid any trace of the previous individual (smell, silk, etc.). To record spider behaviour during trials we used a Logitech c 920 HD Pro webcam attached above the arena. Variables measured were: first choice (area toward which the spider first left the runway) and the proportion of time spent in each area after jumping off the runway.

We used a Chi-squared test of independence to compare the number of individuals that left the starting platform towards either the low drop or the high drop. Because one spider climbed up the arena wall before the 5 min test period had elapsed, we used a paired t-test to compared the proportion of time spent in the low drop and in the high drop.

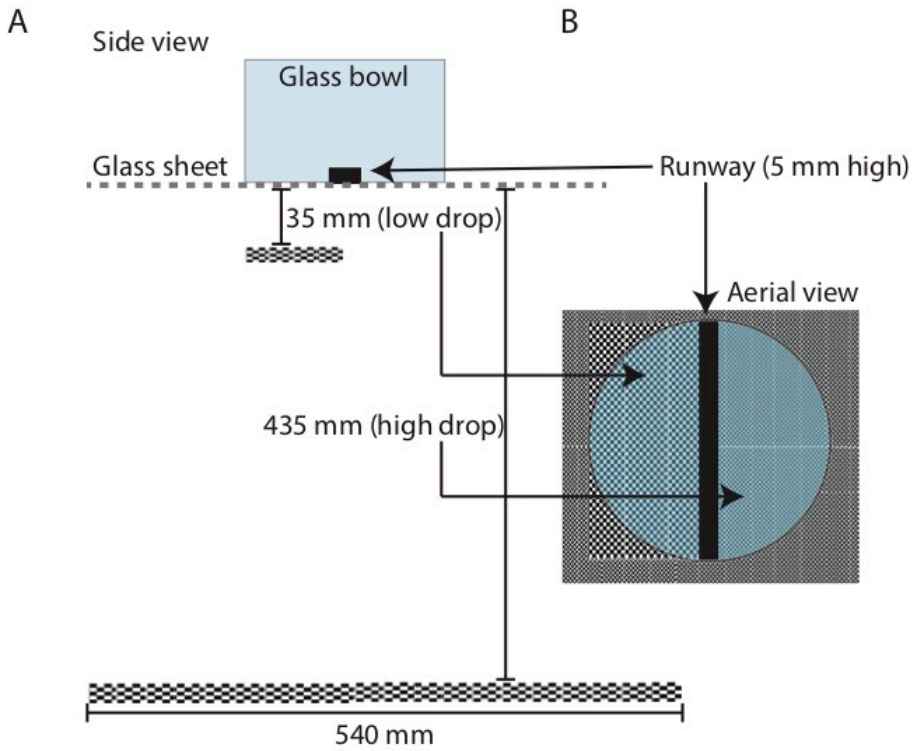


Figure 3. Test arena for Experiment 2. (**A**) Side view of the arena. The spider is positioned over the runway at the start of the trial. (**B**) Top view of the arena. In order from top to bottom the components are: glass bowl to enclose spiders, runway, glass sheet, low drop, and high drop.

Experiment 3. Variation of the visual cliff experiment

To determine if salticids can estimate depth by using only the texture density we modified Experiment 2. Here, we made the height of both drops the same (40 mm) but used different texture densities to simulate different heights: a 'low drop pattern' consisted of 5 mm squares, as used in in Experiment 2 (visual angle 7.15°), while the 'high drop pattern' had 0.5 mm-size squares in a checkerboard pattern (simulating the size of the 5 mm squares being 440 mm away from the spider, visual angle = 0.65°). As in Experiment 2, we used a starting platform over a glass sheet visually dividing both areas and used a glass bowl smeared with petroleum jelly to keep the spiders within the arena.

We used 29 *Trite planiceps* individuals (13 females, 11 juveniles, and 5 males), of which 18 were previously used in Experiment 2 three weeks prior. Trials lasted 5 min from when the spider left the starting platform. We used a Chi-squared test of independence to compare the number of individuals that moved from the starting platform to the big square area or the small square area. As no spiders ended the trial before the five min cut-off had elapsed, we compared the cumulative time in each area using a paired t-test.

Experiment 4. Testing physical depth differences in the gap between platforms

This test was performed to define 1) if salticids change their behaviour according to absolute depth, 2) if salticids use either a monocular or a binocular mechanism for absolute depth perception in the AME, and 3) to rule out the use of stereopsis (based on the ALE) as the main depth perception mechanism. The experimental setup consisted of an aquarium (1200 x 620 x 700 mm high) with two platforms, a starting platform angled at 45° and a flat landing platform at a 50 mm distance (as in Experiment 1). Here, both platforms were 440 mm above the bottom of the aquarium, and the water level was 5 mm below the platforms. As in Experiment 2, we physically varied the depths between the platforms instead of varying the texture density of the substrate. Consequently, the 'low-drop gap' consisted of a laminated texture placed along one half of the gap at a distance of 40 mm below the platforms, and the 'high-drop gap', on the other half, was 440 mm below the platforms (**Figure 4**). Both depth substrate textures were the 5 mm square checkboard pattern used in Experiment 2 (**Figure 2C**). Because of the absolute distances of each substrate depth, the subtended visual angle of the pattern from the spider's point of view corresponded to the high drop and low drop of Experiment 2 (7.15° and 0.65°, respectively).

The experimental design consisted of three spider treatments: 1) control: vision-intact individuals, 2) monocular treatment: spiders with both ALE and one AME occluded, and 3) binocular treatment spiders with both ALE occluded and both AME intact. Occlusion of the ALE was important to prevent depth perception from stereopsis in these eyes, as it is a potential binocular mechanism (Land 1985b) due to the large region of overlap between both ALE (c. 25° in *T. planiceps*, Forster 1979). In the binocular vision treatment we cannot rule out binocular cues from convergence by the two AME because we could not occlude both of these eyes and still have spiders behave in a normal manner (Zurek et al. 2010; Ximena Nelson, unpubl. data). However, the monocular vision treatment rules out both convergence and stereopsis.

Occlusion of the spider's eyes was achieved by the application of an opaque, non-toxic, and removable dental silicone (Coltène Whaledent President light body polyvinyl siloxane; aka 'green gunk') which is harmless to the spider (Zurek et al. 2010). To control for manipulation and for the weight of the silicone, control spiders were manipulated in exactly the same manner, except that instead of covering the eyes, the silicone was placed onto the posterior portion of the cephalothorax. We used 31 spiders (12 females, 14 juveniles, and 5 males), randomly assigning each spider to one of the three treatments. Being a paired test, spiders were used three times (once for each treatment). The order of the treatments in which each spider was tested randomised. The treatment side (left or right from the platform) was randomised between trials, as was as the occluded AME in the monocular vision only treatment. Trials ended after the spider jumped to

the landing platform, or after 90 min had elapsed. The recorded variables were latency to jump (s), chosen area of jump (over low drop or over high drop gap), jump outcome (if the jump was successful (i.e., the salticid landed on the landing platform)), number of random jumps (described in Experiment 1) towards the high drop gap and number of random jumps towards the low drop gap.

We performed a Chi-square test of independence for the number of jumps over each drop (high and low) for each treatment. We also ran Wilcoxon matched-pairs signed rank tests with the total number of random jumps (per spider) towards each drop for each treatment. A second series of Chi-square tests was performed to determine if the different treatments affected jump outcome (i.e., failed jumps towards the landing platform could be interpreted as a miscalculation of the landing platform's distance). We used a Linear Mixed Effects (LME) model, implemented under Restricted Maximum Likelihood (REML), to assess if latency to jump was affected by treatment. The selected model accounted for latency to jump (log-transformed) as the response variable, the treatments (control, monocular treatment, and binocular treatment) as fixed factors, and the individual spiders as the random factor. For plotting, we used the R packages 'nlme' (Pinheiro et al. 2018) for analyses and 'ggplot2' (Wickham 2009) and 'ggpubr' (Kassambara 2018).

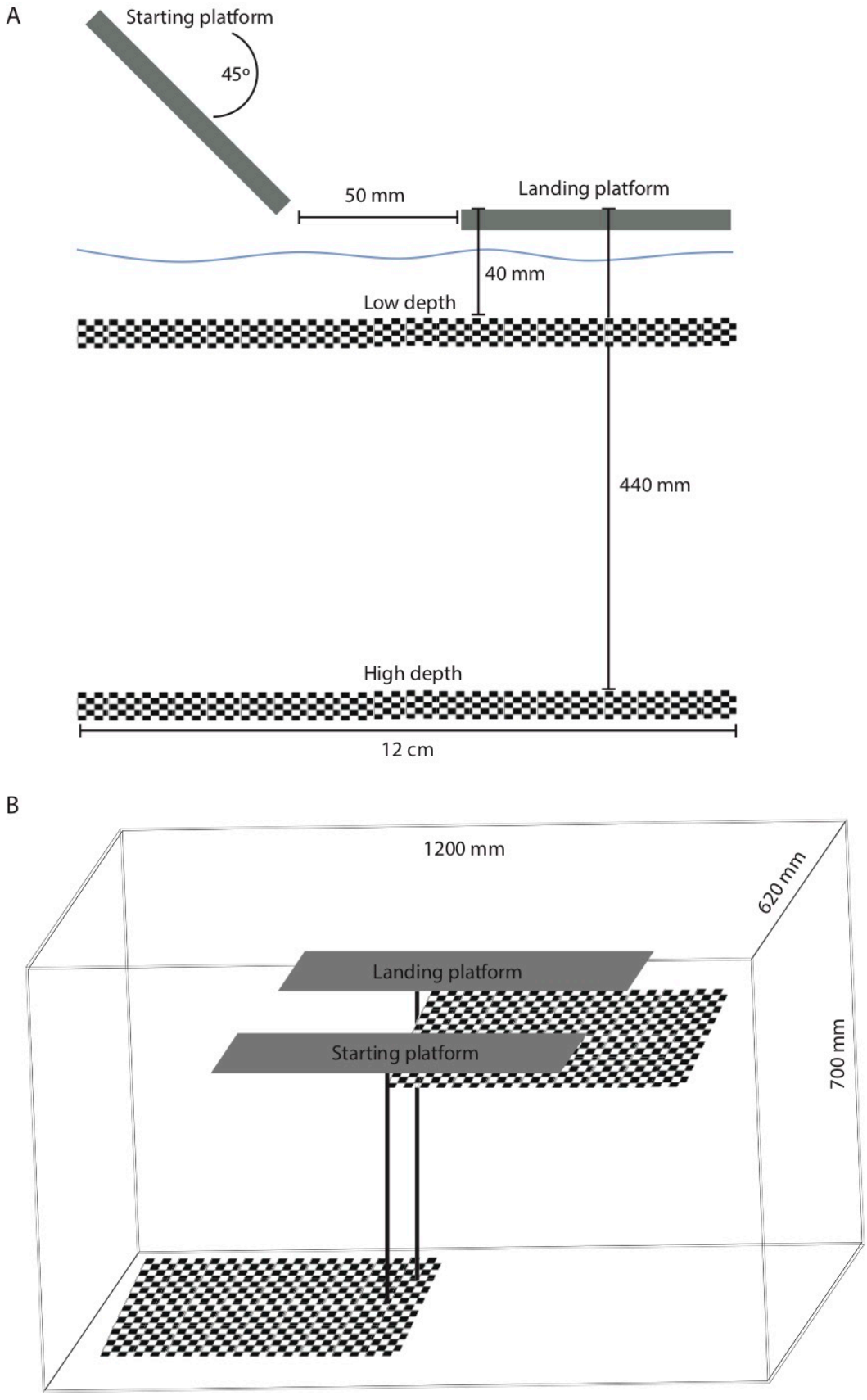


Figure 4. Test arena for Experiment 4. (**A**) Side view of the setup. (**B**) Bird's eye view of the aquarium, low depth on the left and high depth on the right.

Results

In Experiment 1, there was no evidence of preference for jumping over the optical illusion (treatment, n = 16) or the control image (n = 13) (χ^2 = 0.31, df = 1, *P* = 0.577) and the latency to jump was not affected by treatment (estimate = -0.468, CI = -1.017 to 0.082, *Z* = -1.67, *P* = 0.095). The total number of random jumps towards each pattern did not differ (W = -22, df = 1, *P* = 0.432) for the control (total = 16, median = 0, min = 0, max = 3), or the optical illusion (total = 12, median = 0, min = 0, max = 2).

In Experiment 2, the probability of moving towards the low drop (n = 25) was significantly higher than that of choosing the high drop (n = 9) (χ^2 = 7.53, df = 1, *P* = 0.006). Nevertheless, the proportion of time spent in relation to the trial duration did not significantly differ between the high and low drop (*t* = 1.388, df = 33, *P* = 0.174).

In Experiment 3, the number of spiders that moved towards the small square area did not differ from the number of spiders that chose the small square area (χ^2 = 0.310, df = 1, *P* = 0.577). Furthermore, there was no significant difference between the times spent in each area (*t* = 0.606, df = 28, *P* = 0.549).

Finally, in Experiment 4, we found that spiders showed no preference to jump over the high or low drop gap in control trials (χ^2 = 1.285, df = 1, *P* = 0.256) or in the binocular treatment trials (χ^2 = 1.285, df = 1, *P* = 0.256), but were significantly more likely (χ^2 = 3.846, df = 1, *P* = 0.049) to jump over the low drop gap in the monocular treatment trials (one AME and both ALE covered). However, there was no difference in the number of successful jumps compared to failed jumps in control (χ^2 = 0.571, df = 1, *P* = 0.449), monocular (χ^2 = 0.153, df = 1, *P* = 0.694), or binocular (χ^2 = 0.571, df = 1, *P* = 0.449) treatments. Latency to jump did not differ significantly between spiders in the monocular and binocular treatments, but these were significantly slower to jump than control spiders (**Figure 5**, **Table 1**). Regarding random jumps, spiders did not show a preference to jump toward the low drop gap (total = 12, median = 0, min = 0 , max = 3) or the high drop (total = 4, median = 0, min = 0 , max = 1) in control trials (W= -30, df = 1, *P* = 0.213), but aimed towards the low drop gap significantly more often in both the monocular (W = -55, df = 1, *P* = 0.002; low drop total = 17, median = 0, min = 0, max = 6; high drop total = 1, median = 0, min = 0, max = 1) and binocular (W = -51, df = 1, *P* = 0.0474; low drop total = 22, median = 0, min = 0, max = 9; high drop total = 4, median = 0, min = 0, max = 2) treatments.

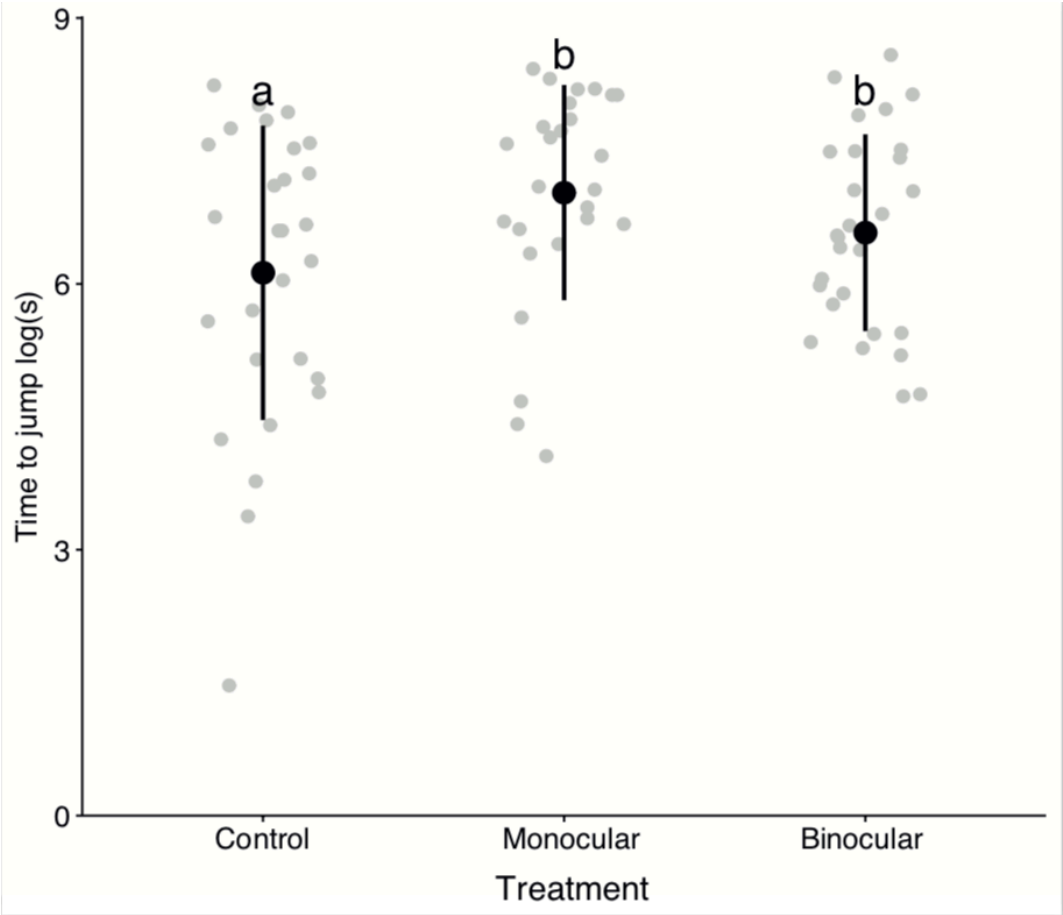


Figure 5. Mean ± standard deviation of log-transformed latency to jump (s) for spiders in three eye occlusion treatments: Control = no occluded yes; Monocular treatment = spiders with one AME and both ALE covered; Binocular treatment = spiders with both AME uncovered, but both ALE covered. Raw data in grey. Different letters represent significant differences between treatments.

Table 1. Results of the LME model. Response variable= latency to jump (log(s)), fixed effect = treatment, random effect = Individuals. 'Individuals' as a random effect explains 6.9% of the overall variance of the data. Presented estimates and 95% confidence intervals (CI) were back-transformed from the log scale.

Fixed effects	**Estimate**	**CI**	**df**	***t***	***P***
Intercept	49.571	42.477 – 57.212	49	26.543	<0.0001
Monocular vs binocular treatment	-0.208	1.347 – 0.060	49	-1.280	0.206
Monocular treatment vs control	-0.866	2.627 – 0.057	49	-2.550	0.013
Binocular treatment vs control	-0.310	1.117 – 0.003	49	-2.198	0.032

Discussion

Condensing the results from our four experiments, we can conclude that texture is used as a monocular cue for depth perception by salticids. Additionally, it is evident that they also possess a mechanism for absolute distance estimation based on monocular cues. Although what these mechanisms might be remain somewhat unclear, our results are consistent with Nagata et al.'s (2012) image defocus hypothesis, where spiders calculate absolute depth by comparing two images of the same scene that are focused differently on photoreceptors on distinctive retinal planes (tiers) in the AME.

Our first objective was to investigate if salticids can perceive the trench illusion as do humans and cephalopods (Josef et al. 2014), predicting that, as salticids also have camera-type eyes, *T. planiceps* would perceive the illusory trench and try to avoid jumping across it. However, spiders showed no tendency to avoid the illusion, suggesting either that they are not fooled by the illusion and thus do not perceive a difference in depth between both visual patterns, or that they perceive the illusion, but as the objective is the landing platform, the height of the gap over which they jump may be considered unimportant. The latter is relevant, as before jumping, salticids commonly attach a silk thread (dragline) to the substrate to avoid an injurious fall to the ground - working as a backup in case of an unsuccessful landing (Chen et al. 2013). To disambiguate between these two possibilities, we ran a visual cliff test to determine whether spiders are aware of, or care about, the height beneath them, finding that indeed, spiders preferred to move toward a low drop instead of a high drop area. This suggests that, while salticids climb high up vegetation, there is an awareness of height and a preference to remain in a 'safer' place.

Aversion to heights is innate in rats, chickens, cats, and humans (Walk & Gibson 1961, Schwartz et al. 1973, Richards & Rader 1983), where it is an important mechanism to enable successful terrestrial locomotion (Walk & Gibson 1961). However, in the visual cliff experiment, salticids did not show a preference to remain in the low drop area. We think that once the spiders stepped off the runway and onto an area, the underlying visual patterns were not clearly visible to the spiders, being distorted by glare from the glass on which they walked. Additionally, being considerably taller than spiders, the vertebrates previously tested all had a perspective of the underlying patterns from above, while the spiders, whose body is extremely close to the ground, would be less likely to perceive the patterns under the glass on which they walked. Moreover, spiders rely greatly on touch, and we observed that once they contacted the glass, aversive behaviour disappeared, suggesting that touch overcomes vision once the spider

is located on a transparent surface. Similarly, rats do not show a preference between high and low drop areas if they can touch the glass directly from the runway (Walk & Gibson 1961).

We wanted to explore the visual texture gradient as an element for depth perception in salticids. A modification of 'visual cliff experiment' (Experiment 3) allowed us to manipulate texture density and rule out several other monocular depth perception cues, such as shadows, occlusion, linear perspective, and image defocus (as the visual patterns were on the same plane). When different texture densities were presented at the same depth under the spider, we predicted that spiders would choose to move toward the big square pattern texture (apparently resembling something closer), rather than the small square pattern. Nonetheless, spiders showed no preference for either of the two pattern densities. The spider's previous experience in the visual cliff experiment (Experiment 2) is unlikely to have affected their behaviour here, as there was a three-week interval between tests and studies on salticid memory have shown retention times of no more than two days being achieved after a 10-hour exposure to an aversive stimulus (Hill 2006, Jakob et al. 2007). Instead, these results are consistent with either stereopsis, or image defocus, which would predict no difference in behaviour, as both patterns were physically at the same depth below the spiders. Indirect support for this conclusion is that, in similar experiments (different texture density but same height), rats (which do not use image defocus) are commonly fooled into the illusion of a greater depth, choosing the area with big squares (Walk & Gibson 1961). However, goats and chickens are not, which has been attributed to the use of motion parallax (a mechanism not used by salticids, Ximena Nelson pers. comm. on unpublished data) or stereopsis as the main depth perception mechanism (Walk & Gibson 1961).

Finally, we aimed to further investigate absolute depth perception in salticids. Two non-mutually-exclusive alternatives exist: image defocus or stereopsis. The former can be achieved with a single eye, while the latter requires two eyes with some separation between them to form disparate images of the same scene. In salticids, this could only be achievable with the ALE, although evidence for stereoscopic vision in salticids is lacking. The design of the Experiment 4 allowed us to limit spiders to monocular depth mechanisms (monocular treatment), binocular depth mechanisms achieved by the ALE or the AME (control trials), or a potential binocular mechanism, such as convergence, mediated through the AME, but eliminating the potential for stereopsis through the ALE (binocular treatment). Unfortunately, it was impossible to test spiders with both AME occluded and leaving the ALE intact because occlusion of both AME results in spiders behaving extremely erratically or simply remaining very still (Forster 1979, Ximena Nelson, unpublished data).

In this final task, depth perception was needed to discriminate between the low drop and the high drop gap beneath the starting platform, as well as to assess the jump from starting platform across the water to the landing platform. We found that salticids assessed distance with monocular vision as accurately as if their vision were not modified. Therefore, there is at least one monocular depth mechanism in salticid vision that spiders rely on to estimate the landing point for targeted jumps. Secondly, in terms of depth awareness, spiders with potential binocular vision through the AME, and those with monocular vision only, exhibited an awareness of the two depths in the gap between platforms, as there were a higher number of random jumps toward the low drop gap, and at least those individuals with monocular vision showed a preference to jump over the low drop gap. Behavioural differences between treatments may be a consequence of the reduction of the field of view by the occlusion of ALE. Although not as spatially acute as the AME, the ALE see in high resolution over a wide field-of-view, while the AME, while enabling higher resolution vision than the ALE, do so only over a field of view of 3-5° (Land 1969a,b, Land 1985a,b). However, in *T. planiceps,* the retinae of the AME can move up to 35° (Forster 1979) on either side of the body axis, but this takes time (Land 1969b), and may explain why in both eye occlusion treatments, in which the wide field-of-view ALE were both covered, the spiders took longer to assess the task before jumping.

Overall, we can infer both that texture as a monocular cue for depth perception is undoubtedly used in salticids, and that there is a monocular depth perception mechanism able to give absolute distance estimations. There are two non-mutually-exclusive monocular mechanisms that could possibly achieve this: accommodation and image defocus. Land (1969a,b), based on measurements from an ophthalmoscope, disregarded accommodation, suggesting that the muscles surrounding the retinal eye tube can only move it laterally or torsionally. Nevertheless, preliminary measurements of the retinae of the AME using an eye-tracker suggest a change of shape in the contour of the retina while looking at stimuli at different depths (Ximena Nelson, pers. comm. on unpublished data), proposing that forward and backward retinal movements (i.e., accommodation) may exist. Depth perception by image-defocus can also explain these findings, and has been demonstrated in salticids (Nagata et al. 2012). Further research is required to determine if accommodation in salticids is possible.

The apparent lack of perception of the illusion among salticids should not be very surprising despite the fact that, like us and like cephalopods, they have camera-type eyes. The ultrastructure of salticid eyes is very different from all other camera-type eyes (Land 1969a, 1985a), and it is very likely that information processing is very different to ours. A recent study revealed that cuttlefish can use stereopsis for depth perception, but the underlying

computational mechanisms whereby this is achieved are different to ours (Feord et al. 2020). The results from this series of experiments further highlight the significant need to better understand the myriad different mechanisms that have evolved to gauge depth among vision-dependent animals.

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CHAPTER SIX. Discussion

Portia fimbriata.

While this thesis began with the main objective to explore the idea that cognition in jumping spiders may have been guided by the complexity of the environment in which the species lives, it also aimed towards doing a comparative study exploring the spatial ability of different species of salticids and their perception in a spatial context. Therefore, the work presented in this thesis is divided in two sections. The first section comprises studies of salticid spatial ability in a comparative cognition framework, exploring detouring in a predatory context (**Chapter 2**) and route planning in a stressful situation (**Chapter 3**). The second section investigates salticid perception in 3-dimensional tasks, firstly by using multimodal cues to assess jumps (**Chapter 4**), and assessing depth using vision (**Chapter 5**).

Main findings

In **Chapter 2**, I tested detouring in two species from different environments: *Marpissa marina* from a rocky shore and *Trite planiceps* from harakeke vegetation (New Zealand flax, *Phormium tenax*). The task required choosing the most efficient route out of four options in order to reach a prey item. We found that *T. planiceps* preferred to choose short routes, but failed to retain a memory of the prey's position, and so failed to prefer to follow routes with prey. In contrast, *M. marina* showed more motivation for routes with lures, but its decision-making was random. Our findings suggest that *T. planiceps* may be more capable at assessing routes than *M. marina*, possibly because the latter species inhabits simple rocky shores, while the former inhabits complex 3D harakeke groves. This idea is supported by experiments with *Portia fimbriata* (Tarsitano & Jackson 1994, 1997, Tarsitano 2006, Cross & Jackson 2016), which inhabits very complex three-dimensional dense vegetation and is able to perform longer detours, maintaining a long retention time regarding a prey's location.

In **Chapter 3**, I evaluated the spatial abilities of two salticid species, *Portia fimbriata* and *Trite planiceps*, but within the context of a stressful scenario. The main task for the test spiders was to find the most efficient, and perhaps less 'risky' route out of four options. As predicted, *P. fimbriata*'s decision-making was better than that of *T. planiceps*, with the former tending to choose the shortest and safest routes in order to escape. Nevertheless, *Trite*'s performance in terms of speed was better than that of *Portia*. Interestingly, rather than follow the pre-defined routes, certain individuals tended to perform novel shortcuts in order to escape. This showed that salticids can make shortcuts in unfamiliar scenarios, framing out the route either beforehand, or at least *en route*. This ability differs from the shortcuts of ants (Wehner & Wehner 1990), bees (Dyer 1991, Menzel et al. 2005, 2011), or other spiders (Seyfarth 1982). In these cases, the individual needs to move around the terrain first and then, by using memory and information based on path integration, it

can trace a shortcut (Wehner & Wehner 1990). This experiment also supports the idea of the Clever Foraging Hypothesis (CFH), as *Portia*'s cognitive abilities outperformed those of *Trite*. In addition, the fact that the spiders tested were able to perform shortcuts endorses the their ability to 'plan ahead of time', as suggested by Cross & Jackson (2016).

In **Chapter 4**, while still focused on spatial abilities, this comparative study investigated the use of multisensory cues when assessing jumps. Spiders had to perform a 5 cm targeted jump with the presence of wind at different speeds. We observed that spiders performed slight adjustments in their position and posture before the jump that depended on the wind, whereas other elements of the jump did not change. Wind awareness was also demonstrated, as in intermittent wind conditions there was a higher probability to jump without wind. Furthermore, contrary to our predictions, *Trite planiceps* performed better than *Portia fimbriata*, having a higher probability to successfully land a jump. *Trite*'s superiority in this task is perhaps explained by its uncommonly high use of non-visual cues in its life history (Taylor et al. 1998, Taylor & Jackson 1999), possibly relying more on mechanoreception than *Portia*. This is interesting, as it is known that *Portia* are adept at using vibratory signals in predation sequences (Jackson & Blest 1982a). Again, the specific characteristics of the environments in which each of these species live may play an important selective role, both in exposure to wind (dense vegetation versus a more open habitat own different wind conditions), and in the use of multisensory cues (*Trite planiceps* is known for its ability to catch prey in the dark, apparently even without chemical cues, Forster 1982).

Finally, in **Chapter 5** we focused on perception, specifically investigating visual depth perception in salticids. Although being far more simple a process than navigation in terms of information processing, the series of experiments performed in this chapter allowed us to gain a deeper understanding of salticid visual perception. Our conclusions indicate that spiders in this family can accurately assess depth by using at least one monocular mechanism, and that one of the visual cues they use to perceive depth is texture density. We discarded the possibility of the use of stereoscopic binocular mechanisms, although spiders with unmodified vision tended to solve the task faster. This does not mean that salticids do not use stereopsis, but that they do not require it. As a collateral effect in order to inspect behaviour under controlled situations, we also demonstrated that salticids are, as a friend said, "scared of heights", having aversive behaviour to high drops.

Future research

One of the species studied in the present series of experiments (*Portia fimbriata*) has been a common denominator in salticid behaviour and cognition studies due to its bizarre combination

of unique attributes: 1) *Portia* is in the Spartaeinae subfamily, which is categorised as a primitive group (Wanles 1978, Su et al. 2007, Maddison et al. 2014), and the genus can be recognised by its use of rudimentary spider webs to nest on and catch prey (Jackson 1982). 2) *Portia*, like other spartaeines, uses vibratory signals for predation significantly more heavily than most modern salticids (Jackson & Blest 1982a). 3) *Portia* also has very acute vision, being able to identify objects at a distance of nearly 30 cm (Jackson & Blest 1982b). *Portia*'s AMEs have a region of 'high spatial acuity' of 0.04º (Su et al. 2007) - this astounding spatial acuity is attributed to having long focal length, a telephoto construction of the eye with a secondary put at the end of the eye tube in which the retina lies, and small, closely-spaced photoreceptors (Williams & Mclntyre 1980). 4) As detailed in **Chapter 1**, this genus specializes on many predatory strategies (Wilcox et al. 1996, Jackson 1992, Harland & Jackson 2006) and excels in certain areas of high-level cognition, such as learning (Jackson & Carter 2001, Jackson & Cross 2011, Jackson & Nelson 2011), spatial memory (Tarsitano & Jackson 1997, Cross & Jackson 2016, 2019), numerical competence (Nelson & Jackson 2012, Cross & Jackson 2017), and possibly even forward-thinking (Cross & Jackson 2016, 2019, **Chapter 3**).

It is important to consider *Portia*'s evolution to understand why it possess such attributes and to ascertain which were the main selective pressures that acted on its clade. Previous studies (Jackson 1982, Jackson & Blest 1982a, Blest & Sigmund 1984, Su et al. 2007, Maddison et al. 2014) have tried to solve the evolutionary history of *Portia*, concluding that the behaviour and phylogeny of Spartaeinae are closely related. Results by Su and colleagues (2014) pointed out that there was a very basal divergence in the Salticidae (diversifying the Spartaeinae from the Lyssomaninae around 41.4 million years ago (mya), Bodner & Maddison 2013), with araneophagic (spider-eating and often web-invading) spiders on one side and cursorial hunting spiders on other side. The araneophagic spiders gradually specialised on predatory tactics, first by invading spider webs to catch prey, and then developing predatory (aggressive) mimicry, and finally achieving high visual acuity (which is considered a convergent attribute being shared with Salticoids (a cursorial group that also diverged at basal stages; Su et al. 2014). In relation to salticid evolution, the next step would be to relate cognition abilities and the evolutionary history within the Spartaeinae to have a better idea about cognitive evolution in this clade.

Unfortunately, integrative studies regarding salticid evolution are scarce in other groups, which mean that making inferences about the evolution of cognition within the whole family can be too speculative. As a consequence, more studies integrating phylogenetic information already available (e.g., Maddison & Heding 2003, Maddison et al. 2008, 2014) with behaviour, morphology,

and cognition will help to understand how the different groups evolved and why this family is so diverse.

In this thesis our approach was to relate spatial ability with environmental complexity, as an indirect clue about salticid evolution. However, because we could only compare the spatial abilities of three spider species from three different natural environments, we cannot categorically conclude that salticid spatial cognition is a consequence of environmental complexity, as replicate species from each environment - at least - is needed to draw solid conclusions. However, in general, our results do support the CFH, spatial ability corresponded with the complexity in which the tested species live. As stated, in order to accept this hypothesis - and discard other plausible selective pressures for the evolution of cognition in salticids - more comparative studies must be made.

Theoretical studies have suggested that the evolution of cognition is faster and evolves towards complexity when a species lives in a complex environment (Godfrey-Smith 1996, 2001). Environmental complexity is defined as a space that varies, that is diverse, that can manifest different stages, or that can 'do' many things (Godfrey-Smith 2001). In other words, it represents heterogeneity in either space or time, or both simultaneously. As a consequence, a comparative cognitive study among an immense number of species is not enough to discern, for example, why *Portia* is so 'smart'. It is paramount to study their own environments and not only their variability at a given time (changes during the day, seasonal changes), but also in geological time. While further analysing the evolution of *Portia fimbriata*, we can observe that the divergence of Spartaeinae as a monophyletic group that specialises on feeding on spiders occurred about 41.4 mya, during the Eocene epoch (Bodner & Maddison 2013). The Spartaeinae evolved from this time until *Portia*'s diversification in the Miocene, around 16 mya, over a timespan of about 26 million years (Bodner & Maddison 2013). With this information, it is possible to analyse the environment dynamics in three different timescales: millions of years, thousands of years, and recent times.

In the Eocene, Australia was already separated from Antarctica, but was still 'drifting' North. At this point, one of the regions in which *P. fimbriata* is currently distributed (North-East Australia) consisted of sub-tropical and tropical rainforests, with 10% of gymnosperms and (now rare) species of *Ephera* and *Banksia* (Kemp 1978). Later on, during the Oligocene, Australia experienced a decrease in plant diversity, perhaps as a response to a drop in temperatures. Finally, during the Miocene, in which the genus *Portia* diversified, the North Australian region became increasingly arid and the Queensland region, remained wet and experienced a peak abundance of *Nothofagus brassi* trees (which became rare at the end of the epoch) and gymnosperms. In summary, the North-East region of Australia did not suffer many structural changes throughout the

evolution of *Portia fimbriata*, but the constant presence of a dense rainforest vegetation (highly complex in structure) may have had an effect as a selective pressure.

On a shorter timescale, vegetation transitions have been very dynamic in the last 38,000 years. From 38,000 to 24,000 years before present (bp), *Araucaria* vine forests and rain forests were common on this region of northern Australia. This flora then transitioned into *Eucalyptus* forest (from 24,000 bp to 6,000 bp), which is highly dynamic, as fire contributes to a constant modification of the landscape. From 6,000 bp onwards another transition into rainforest occurred, and formed the current rainforest vegetation (Hopkins et al. 1993).

At an even shorter timescale, the current Queensland rainforest varies greatly in structure and composition: it has 27 different rainforest community types and complexes (Webb et al. 1984). These are very dynamic due to the presences of fires, which give rise to different stages of 'transitional mixtures' (Webb & Tracey 1981). Even though *Portia* diversification was already established in the Miocene, the shorter series of changes in vegetation (from several thousand years ago until now) may have caused behavioural (and even cognitive) differences between the *P. fimbriata* population that lives in Queensland, compared to populations located in other regions (Nepal, India, Sri Lanka, Taiwan, Indonesia; World Spider Catalog 2020). For example, behavioural variations in predation have been demonstrated in different populations of *P. labiata*, despite the fact that these populations are located in the same region, but in diverse environments (Jackson & Carter 2001, Jackson et al. 2002). Furthermore, within-species differences in predatory behaviour have been observed in *P. fimbriata* while preying on another salticid (*Euryattus* sp.), with the population that normally feeds on this prey adopting a specific predatory strategy compared to the other *P. fimbriata* populations (Jackson & Hallas 1990). These examples demonstrate that behavioural differences at intra-specific level are also significant, and that these could apply to populations residing in distinct environments.

As an extra level of complication, it is likely that other selective factors, such as prey availability, inter-specific competition, and predator presence may have simultaneously affected salticid evolution. So far, our inferences have been focused on how environmental complexity in a 'structural' sense (height, density and spatial intricacy of the vegetation and abiotic elements) might affect salticid cognition. However prey availability, for example, may have played an important role in the evolution of salticid cognition. In the case of *Portia* evolution, it has been argued that the scarcity of insects and high density populations of other spiders living nearby could have affected *Portia*'s evolutionary history to evolve into a specialised spider-eating predator (Jackson 1982, Jackson & Blest 1982a, Blest & Sigmund 1984, Su et al. 2007). Thus, living among other spider species (dangerous prey) and constantly interacting with different spider webs

represents a very unique type of environmental complexity which may have affected the evolution of visual ability and predatory behaviour. Overall, these findings support the CFH to explain cognition among the Spartaeinae.

In conclusion, comparative studies related to the CFH would be more robust if different levels of environmental complexity (i.e., vegetation structure and dynamics, prey availability, predation presence, etc.) are taken into account.

In this thesis I adopted methodology that historically has been used only in vertebrates. For example, the pool experiments performed in **Chapter 3** possess similar features as the Morris water maze, in which rats are tested for cognitive purposes (e.g., reference memory, spatial working memory, learning) under a stressful, but harmless, scenario (presence of water)(Morris 1981, Sharma et al. 2010). The benefit of this arena is that, despite being a negative stimulus, the tested individuals are not harmed. In contrast to the use of heat, electric shocks, or being exposed to dangerous prey, the 'pool experiment' has a great potential for learning tasks in jumping spiders, as individuals can be re-tested many times.

The novel implementation of the visual cliff experiment with spiders (and more broadly, in invertebrates) is also very useful, not only for depth perception research, but also for spatial awareness. Its simplicity and efficiency in behavioural tests allows it to be implemented for different species of invertebrates and for species with different visual perception. Thus, the next step to fully understand salticid depth perception is to discover which monocular mechanism is acting mainly to estimate depth. Specifically, the mechanisms that we could not rule out were image defocus, and accommodation.

Unfortunately, we could not demonstrate if salticids perceive the illusion as cuttlefish and humans do. Nagata and colleagues (2012), using physiological tools, and then Guo and colleagues (2019), applying the theory to a physical mechanism, demonstrated the maximum capabilities of AME to register visual stimulus. Nevertheless, it is difficult to make inferences about perception without understanding the perceptual filtering of the information received by the eye and how this ultimately translates into behaviour. Therefore, the continuation of behavioural observations on visual perception (multisensory perception, to a greater extent) are paramount to scrutinise visual perception, and how the different visual cues interact simultaneously in the spider's nervous system.

Although it was believed that vertebrates were the only animals with a nervous system complex enough to have cognitive abilities, in the recent decades the definition of 'cognitive

animal' has been given to a wide variety of taxa, including those with very basic forms of nervous system (e.g., earthworms, *Aplysia*)(Bekoff et al. 2002). In the present thesis, I have demonstrated the existence of complex cognitive abilities in salticids: visual assessment (detour distance, detour that leads to prey, etc.), the use and processing of multisensory information (wind and vision perception to calculate a targeted jump), and potential forward-planning (shortcuts without previous experience). These results show how complex the behaviour of these little creatures can be. In my view, the mere possibility of episodic-like memory occurring in the tiny brains of spiders is astonishing, and despite the fact that the information-processing ability is nowhere near those of the human brain, this could be an example of convergent evolution.

Convergent traits are those that evolved independently, resulting in similarities among non-related taxa. The greater the phylogenetic separation between the taxonomic groups, the stronger the convergence (Marino 2002). Convergence is a process that can take place at many levels, such as structure (eye) and function (flying), in morphology, physiology, simple behaviours, or higher-level complex cognitive characteristics (Marino 2002). It has been argued that intelligent behaviour is represented in many different groups and are examples of convergence of cognition due to the independent formation of complex brain or brain-like structures. This independent development is believed to have started before the divergence between deuterostomes and protostomes, as the common ancestor of both groups already had a brain (Roth 2015).

Examples of intelligent cognitive behaviour span across extant taxa and encompass a variety of neural platforms that enable this type of behaviour. For example, in invertebrates, cephalopods have a very complex nervous system consisting of a brain divided into 16 lobes and a neural network of 550 million neurons distributed in the eight arms (Hochner et al. 2006), while in insects, morphological differences in the mushroom bodies show convergence among blattoids, dipterans, and hymenopterans. Differences in neuroanatomy underpinning cognitive behaviour also exist in vertebrates. For example, in cichlids the medial pallium has developed four new ventrolateral zones in the brain, and corvids and other birds have seen the evolution of the nidopallium and mesopallium areas (Rehkämper 1991, Reiner et al. 2004, Güntürkün 2012), while in cetaceans we find the presence of a paralimbic region (Marino 2002), and in primates we see an expansion of the prefrontal complex (Roth 2015).

The presence of high-order cognitive processes in different taxa further adds to this complexity, but are also likely to be examples of convergent evolution. Such cases are observed in corvids (tool-use and mental time travel, Emery & Clayton 2004), cetaceans (complex social behaviour, 'language' comprehension and self-recognition, Marino 2002), primates (extended working memory, tool use, self-recognition, etc.), and in certain species of salticids (learning, spatial

memory, numerical competence, and probably forward thinking Tarsitano & Jackson 1997, Jackson & Carter 2001, Jackson & Cross 2011, Jackson & Nelson 2011, Nelson & Jackson 2012, Cross & Jackson 2016, 2017, 2019). Thus, I can't help but think that the fact that we see semblances of higher-order cognition in salticids may actually be a striking case of cognitive convergence in which complex behaviours also evolved independently, despite profound neuroanatomical differences.

So far, the evolution of cognition has been justified in terms of brain structure and complexity. In bees, the brain has had great modifications: the mushroom bodies occupy half of the brain of the bee and possess dense arrays of Kenyon cells (which mediate learning in bees), with a neural density 15 times higher than the highest neural densities found in the vertebrate brain (Roth 2015). However, in smaller invertebrates, evolution towards a more complex nervous system cannot always be afforded, despite the need for complex behaviour. More complex cognitive behaviours commonly require more energy due to an increase of neuronal activity, especially in small animals (Durst et al. 1994, Gronenberg et al. 1996, Eberhard 2007). Consequently, it could be possible that, in animals with less complex brains but that still display complex behaviours, rather than leaning towards greater brain complexity and bigger brains, evolution may have been diverted towards simplification of the processing of information.

The theory of 'economy of design' suggests that small brains can be more efficient through different mechanisms: from cellular-level functionality changes (Bullock & Horridge 1965, Altun & Hall 2008), to the elimination of redundancy (Bernays & Wcislo 1994, Niven 2010) and the simplification of information-processing (Eberhard & Wcislo 2011). Failed attempts to demonstrate a correlation between more simple behaviour and brain miniaturization in orb-web spiders (Eberhard 2007, Eberhard & Wcislo 2011), termites (Howse 1974), ants (Wilson 1984), and first-instar strepsipteran larvae (Beutel et al. 2005) supports this idea. Furthermore, in spiders, a large part of input processing, including sensory perception and motor processes (Barth 2002, Chapman 1982), is done at peripheral neural levels, allowing the economization of brain tissue. In salticids, a large portion of the brain is dedicated solely to visual processing (Steinhoff et al. 2017, 2019) which leaves less neuronal material destined for the rest of the functions. Consisting of a comparatively small brain, it is possible that the pathway for information processing towards high level cognitive behaviours in salticids are greatly simplified compared to those exhibited in humans, but with similar results. Thus, I suggest that cognition in *Portia* and apes must have evolved through a process of divergent brain evolution resulting in similar behaviours, with completely different information-processing mechanisms, and perhaps without the need to develop high complexity

within the spider brain to achieve such behaviours. Undoubtedly, more studies, such as those recently performed by Steinhoff and colleagues (2017, 2019) on neural/'brain' physiology and how information is processed in such miniature systems could help support or refute this idea.

Navigation studies in invertebrates have been made primarily on bees (e.g. Dyer 1996, Fry and Wehner 2005, Riabinina 2014) and ants (e.g. Collet et al. 1998, Collet 2012, Wehner et al. 2016, Narendra et al. 2017, Schwarz et al. 2017), and to a lesser extent in some arachnids, such as amblypygids (Hebets et al. 2014a,b) and the Namibian desert spider (e.g. Nørgaard 2005, 2006, 2007, 2008). Salticids also represent an ideal system to study navigation, as these are guided mainly by vision, have multisensory perceptual abilities, are diurnal predators, and they wander around by themselves (Foelix 2011). As ethologists, we are just starting to scratch the surface of salticid navigation, being able to demonstrate the use of shortcutting, assessment of different levels (risk, distance, depth), and orientation by vision. These capabilities are comparable to those of bees or ants, but are perhaps different from insects and vertebrates in the ways in which they perceive and process information. In the spatial tasks we did here, we pushed the limits of spatial memory for *T. planiceps* and *M. marina*, but other areas can be further exploited. For example, whether salticids can make shortcuts of a greater scale than the pool used here would be interesting to further explore. Additionally, comparative studies in navigation could contribute toward solving the discussion about the existence of cognitive maps, which is still a subject of dispute (Wehner & Menzel 1990, Wehner & Wehner 1990, Bennet 1996, Foo et al. 2005, Chesseman et al. 2014, Cheung et al. 2014).

Cognitive ethologists have been striving toward the recognition of animal cognition as an observed phenomenon across many taxa (Bekoff et al. 2002). In recent years, high-order cognitive abilities have been discovered not only in non-human vertebrates (e.g., Menzel 2005, Taylor et al. 2007), but also in invertebrates (e.g., Pahl et al. 2007, Dacke & Srinivasan 2008, Cross & Jackson 2016, Chittka 2017). To the present day, there is still a lot of discussion, and objection, about the study of consciousness, self-awareness (Hauser 2000), mental time travel (Bischof 1978, Roberts 2002, Tulving 2005, Suddendorf & Corballis 2007; but see Shettleworth 2010, Menzel 2005, Redish 2016), metacognition (Carruthers 2008, Jozefowiez et al. 2009, Crystal & Foote 2009, Smith et al. 2009, Carruthers & Ritchie 2012, Crystal 2012; but see Proust 2013), and intentionality (Rosenberg 1990) in non-human animals. Nevertheless, I am confident that studies like the ones presented in this thesis will change the balance in favour of the acceptance of the possibility of at least some

higher-order cognition in invertebrates, and engender more interest in the myriad forms of cognition and complex behaviour exhibited by these fascinating little beasts.

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APPENDIX 1. Chapter 2

1.1Number of re-orientations

We recorded the 'number of re-orientations' performed by each spider during the trials. This variable is defined as the number of turns towards the goal platform when the spider was on the floor of the arena. Re-orientations were performed once the salticid had decided and begun a detour, thus no longer having visual contact with what was on the goal platform and providing a measure of motivation to follow the route.

We compared the number of re-orientations using GLMs with a Poisson distribution separately for each species. For *Trite*, the explanatory variables were spider category and the route choice. For *Marpissa*, we used spider category, route choice and the giving up point as explanatory variables, and no interactions were accounted for. Contrast tests were then applied with the 'gmodels' package.

Re-orientations appear to be an indicator of motivation to complete a route: of the 116 tested spiders across both species, 57% of those that completed routes (n = 74) re-oriented, while 21% of the 42 spiders that did not complete routes re-oriented (X^2 = 13.574, $P < 0.0001$). We found no significant differences in the number of re-orientations between *Trite* and *Marpissa* (estimate = 0.02, Z = 0.087, P = 0.930). However, the number of re-orientations in *Trite* significantly differed by spider category, being higher in males than in females (**Figure 1A**). Furthermore, spiders that chose the short-control route had the lowest number of re-orientations (**Figure 1B**, **Table 4**). Platform re-orientations differed in *Marpissa* depending on chosen route, being lower with the short control route compared with the other routes (**Figure 2A**). Moreover, *Marpissa* showed a higher number of platform reorientations when the individuals completed the route compared with those individuals that did not reach the goal platform (**Figure 2B**, **Table 5**).

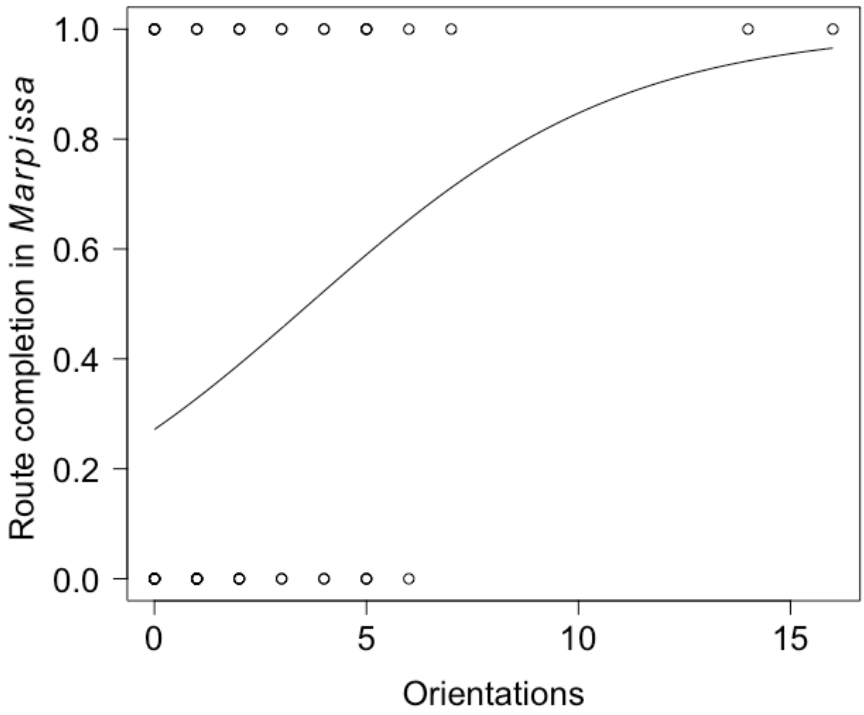

Figure 1. Binary logistic regression of the relationship between the number of orientations and route completion in *Marpissa*. 0 = incomplete routes, 1=complete routes.

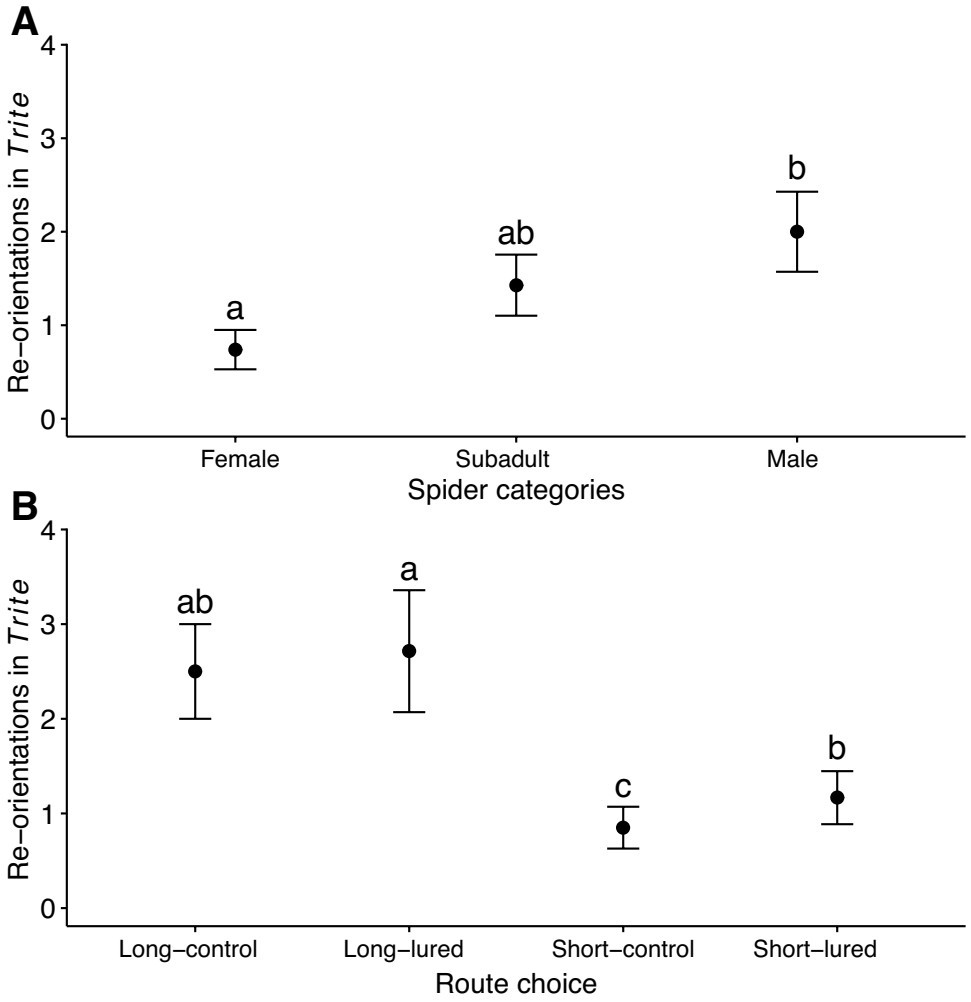

Figure 2. Mean (±SEM) number of re-orientations in *Trite* by (**A**) spider category, and (**B**) chosen route. Note that long-control routes were marginally non-significant compared with short-lured routes ($P = 0.07$). Letters indicate significant differences between groups.

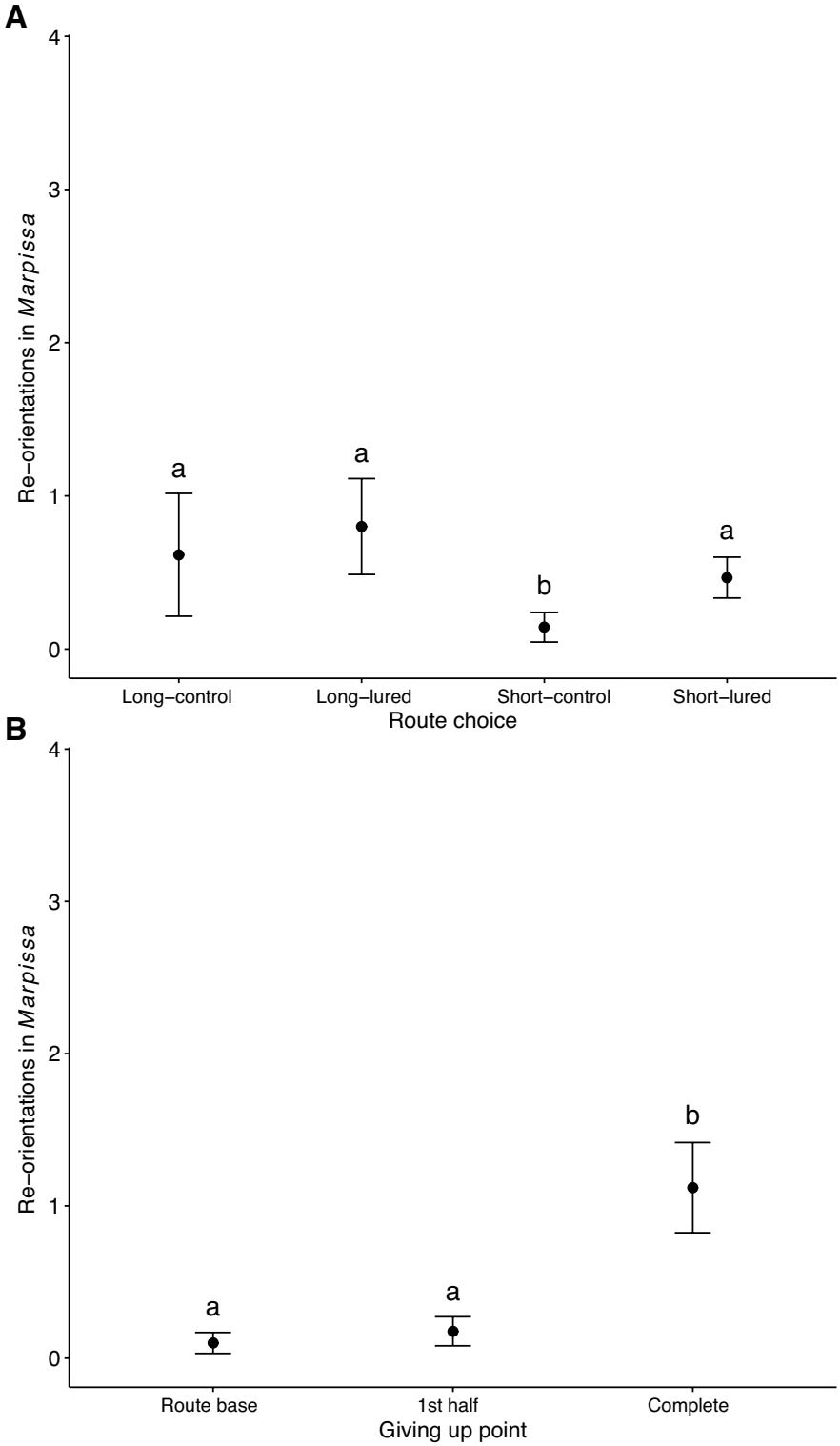

Figure 3. Mean (±SEM) number of re-orientations made by *Marpissa* by (**A**) chosen route, and (**B**) giving up point. Categories: reaching the base of the chosen route; reaching the first half of the route; completing the route (reaching the lure platform). Category of reaching the second half of the route is not shown as all spiders that got to this point completed the route. Letters indicate significant differences between groups.

Table 1. Percentages (n in parenthesis) of *Trite* and *Marpissa* choosing each route.

Trite planiceps				
Motivation	**Short control**	**Short-lured**	**Long control**	**Long-lured**
Decided	29 (7)	5 (12)	4 (1)	17 (4)
Undecided	47 (8)	35 (6)	6 (1)	12 (2)
Marpissa marina				
Decided	5 (1)	30 (6)	20 (4)	45 (9)
Undecided	32 (8)	20 (5)	20 (5)	28 (9)

Table 2. Effect of chosen route and spider category on the number of orientations in *Trite*. CI = 95% confidence interval.

Variables	Estimate	CI	Z	*P*
(Intercept)	1.254	0.491 – 1.886	3.563	0.0003
Route [long-lured]	0.066	-0.654 – 0.884	0.172	0.860
Route [short-control]	-0.881	-1.572 – -0.084	-2.35	0.018
Route [short-lured]	0.081	-0.558 – 0.847	0.231	0.817
Category [subadult]	0.448	0.081 – 0.812	2.409	0.015
Category [male]	0.033	-0.345 – 0.406	0.175	0.861
Contrast tests				
Comparisons	Estimates	CI	X^2	*P*
Long-lured/Short-control	0.948	0.441 – 1.455	14.014	0.0001
Long-lured/Short-lured	-0.015	-0.409 – 0.439	0.005	0.943
Short-control/Short-lured	-0.963	0.564 – 1.362	23.285	<0.0001

Table 3. Effect of chosen route, spider category, and giving up point on the number of orientations in *Marpissa*. Giving up point: 2 = reaching up to half-way up the route; 4 = reaching the goal platform. CI = 95% confidence interval.

Variables	Estimate	CI	*Z*	*P*
(Intercept)	0.429	-0.122 – 0.982	1.525	0.127
Route [long-lured]	-0.127	-0.682 – 0.426	-0.452	0.651
Route [short-control]	-0.139	-0.717 – 0.439	-0.472	0.637
Route [short-lured]	0.228	-0.307 – 0.764	0.836	0.403
Category [subadult]	-0.23	-0.704 – 0.244	-0.951	0.341
Category [male]	0.115	-0.333 – 0.564	0.503	0.615
Giving up point [2]	-0.054	-0.599 – 0.491	-0.194	0.846
Giving up point [4]	0.492	0.028 – 0.957	2.08	0.037

Table 4. Effect of chosen route and spider category on the number of re-orientations in *Trite*. CI = 95% confidence interval.

Variables	Estimate	CI	*Z*	*P*
(Intercept)	0.593	-0.379 – 1.565	1.196	0.231
Category [subadult]	0.566	-0.093 – 1.226	1.168	0.092
Category [male]	0.858	0.238 – 1.479	2.712	0.006
Route [long-lured]	-0.285	-1.329 – 0.758	-0.536	0.591
Route [short-control]	-1.187	-2.197 – -0.176	-2.302	0.021
Route [short-lured]	-0.89	-1.889 – 0.095	-1.772	0.076
Contrast tests				
Comparisons	Estimate	CI	X^2	*P*
Subadult/Male	-0.292	-0.899 – 0.314	0.928	0.335
Long-lured/Short-control	0.901	0.205 – 1.596	6.716	0.009
Long-lured/Short-lured	0.611	-7.22e-05 – 1.222	3.999	0.045
Short-control/Short-lured	-0.289	-0.917 – 0.337	3.187	0.001

Table 5. Effect of chosen route, spider category, and 'giving up point' on the number of re-orientations in *Marpissa*. Giving up point: 2 = reaching up to half-way up the route; 3 = reaching the second half of the route; 4 = reaching the goal platform. CI = 95% confidence interval.

Variables	Estimate	CI	*Z*	*P*
(Intercept)	-1.643	-3.150 – -0.137	-2.139	0.032
Category [subadult]	-1.012	-2.128 – 0.103	-1.778	0.075
Category [male]	-0.539	-1.360 – 0.282	-1.286	0.198
Route [long-lured]	-0.010	-0.876 – 0.854	-0.024	0.980
Route [short-control]	-2.008	-3.581 – -0.435	-2.503	0.012
Route [short-lured]	-0.625	-1.693 – 0.442	-1.148	0.251
Giving up point [2]	0.785	-1.037 – 2.608	0.845	0.398
Giving up point [3]	-13.635	-4136 – 4108.88	-0.006	0.994
Giving up point [4]	2.550	1.092 – 4.008	3.428	0.0006

Table 6. Summary of Accelerated Failure Time models for scanning duration using the general dataset (Weibull distribution) and the data from spiders that completed routes (i.e., excluding spiders that did not reach the lure platform; loglogistic distribution). Scanning duration as a function of route choice, spider category and species. Interactions were not accounted for in the model. CI = 95% confidence interval.

General dataset				
Variable	Estimate	CI	*Z*	*P*
Intercept	6.052	5.397 – 6.707	18.11	<2e-16
Route [long-lured]	-0.084	-0.857 – 0.689	-0.21	0.831
Route [short-control]	-0.478	-1.222 – 0.264	-1.26	0.206
Route [short-lured]	-0.361	-1.088 – 0.365	-0.97	0.329
Species [*Trite*]	-0.666	-1.134 – -0.199	-2.80	0.005
Category [subadult]	-0.578	-1.135 – -0.021	-2.03	0.042
Category [male]	-0.236	-0.768 – 0.302	-0.85	0.394
Log(scale)	0.175	NA	2.47	0.013
Completed routes dataset				
Intercept	6.321	5.278 – 7.364	11.88	< 2e-16
Route [long-lured]	-1.100	-2.296 – 0.096	-1.80	0.071
Route [short-control]	-0.958	-2.056 – 0.139	-1.71	0.086
Route [short-lured]	-1.010	-2.089 – 0.068	-1.84	0.066
Species [*Trite*]	-0.657	-1.243 – -0.071	-2.20	0.027
Category [subadult]	-1.00	-1.576 – -0.423	-3.40	0.0006
Category [male]	-0.463	-1.094 – 0.166	-1.44	0.149
Log(scale)	-0.487	NA	-4.97	6.6e-07

Table 7. Summary of Accelerated Failure Time models for route duration using the general dataset (loglogistic distribution). Route duration as a function of route choice, spider category and species. Interactions were not accounted for in the model. CI = 95% confidence interval.

Variable	Estimate	CI	*Z*	*P*
Intercept	5.516	5.070 – 5.962	24.23	<2e-16
Route [long-lured]	0.129	-0.385 – 0.643	0.49	0.623
Route [short-control]	-0.249	-0.754 – 0.257	-0.96	0.335
Route [short-lured]	-0.266	-0.758 – 0.227	-1.05	0.291
Species [*Trite*]	0.127	-0.168 – 0.422	0.84	0.399
Category [subadult]	-0.073	-0.415 – 0.269	-0.42	0.677
Category [male]	-0.358	-0.683 – 0.032	-2.16	0.031
Log(scale)	-0.839	NA	-10.75	<2e-16

Table 8. Summary of Accelerated Failure Time models for route duration using data excluding spiders that did not reach the lure platform (lognormal distribution). Route duration as a function of route choice, spider category and species. Interactions were not accounted for in the model. CI = 95% confidence interval.

Variable	Estimate	CI	*Z*	*P*
Intercept	6.571	6.097 – 7.045	27.19	< 2e-16
Route [long-lured]	-0.198	-0.750 – 0.352	-0.71	0.479
Route [short-control]	-0.606	-1.103 – -0.110	-2.39	0.016
Route [short-lured]	-0.725	-1.217 – -0.232	-2.89	0.003
Species [*Trite*]	-0.618	-0.903 – -0.334	-4.27	2.0e-05
Category [subadult]	0.152	-0.142 – 0.447	1.02	0.309
Category [male]	-0.324	-0.634 – -0.013	-2.05	0.040
Log(scale)	-0.611	NA	-7.43	1.1e-13
Specific comparisons				
Long-lured/Short-control	-0.408	-0.823 – 0.007	-1.92	0.055
Long-lured/Short-lured	-0.526	-0.936 – -0.116	-2.51	0.012
Short-control/Short-lured	-0.118	-0.399 – 0.163	-0.82	0.410

APPENDIX 2. Chapter 3

Experiment 1

2.1 Establishing the use of first or last attempt data for analysis

One of the unexpected behaviours observed in the trials was the use of more than one route throughout a single trial by some individuals. Spiders sometimes chose a route but then returned to the starting platform before completion and chose a different route (or the same route for again) to exit. The number of attempts before escaping the pool ranged from one (completion of the route on the first time) to three (two incomplete routes and one final complete route). Because of this, the results could have changed when using last attempt data (data from completed routes only) or when using first attempt data (data from the first attempt, including individuals that completed and those which did not complete the route). Therefore, we investigated whether the probability to choose the safe route differed between first and last attempt using McNemar's exact test with central confidence intervals (Fay 2010). We found no differences, either for *Portia* (sample estimates: 0.2, n = 62, Confidence Interval [CI] = 0.004 – 1.787, $P = 0.218$; **Figure 1**) or for *Trite* (sample estimates = 0.5, n = 47, CI = 0.008 – 9.604, $P = 1$; **Figure 2**) of the probability to choose safe routes between both datasets. Accordingly, all further analyses were based on data obtained from the last attempt, as this dataset was larger (N = 87), than first attempt data (n = 66).

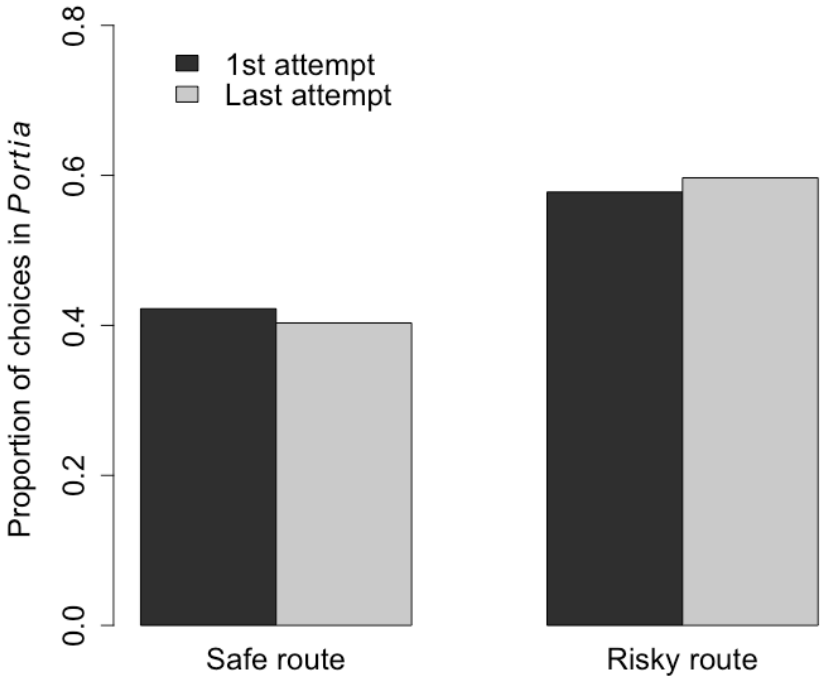

Figure 1. Proportion of *Portia* spiders using either the risky or the safe route based on data from both the first and last attempt to exit the arena in Experiment 1.

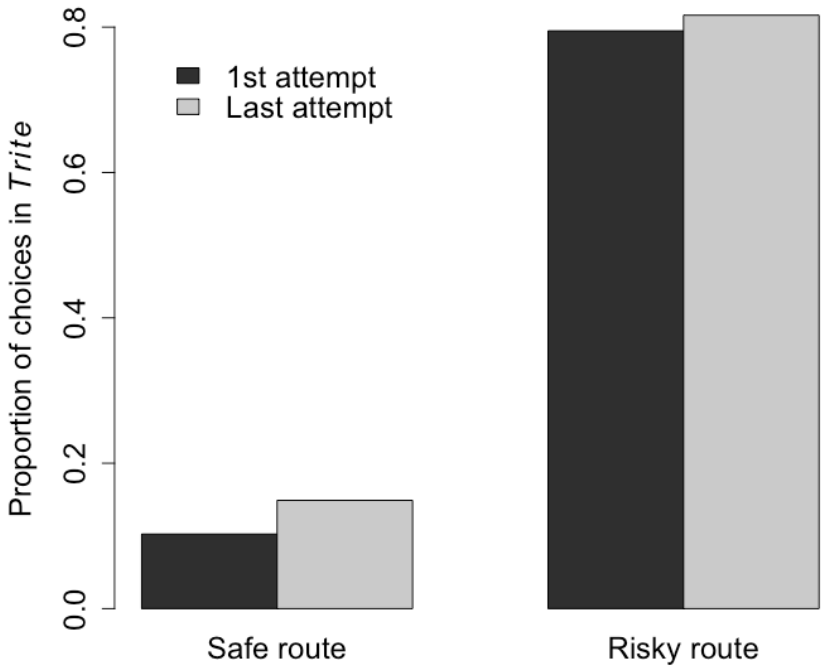

Figure 2. Proportion of *Trite* spiders using either the risky or the safe route based on data from both the first and last attempt to exit the arena in Experiment 1.

Table 1. Results of the generalized linear model of number of the proportion of dowels used by spiders while escaping a function of spider category (females, subadults, and males), spider species (*Portia* and *Trite*), Route choice (safe, risky), and direction of the pool (North, South, West, and East). CI = Confidence interval at 95%. "[]" indicates a specific category of each variable. Estimates and CI of estimates from Wald tests. NA: no estimates for 'route choice'/'male category' interaction, due to none of *Trite* males chose the safe route.

Variable	**Estimate**	**CI**	***t***	***P***
Intercept	1.443	0.266 – 2.820	2.250	0.026
Category [Subadult]	0.652	-0.688 – 2.010	0.961	0.338
Category [Male]	0.527	-1.968 – 0.867	-0.737	0.462
Route choice [Safe]	0.205	-1.565 – 1.139	0.301	0.764
Species [*Trite*]	1.495	-0.081 – 3.401	1.748	0.083
Direction [N]	0.673	-2.011 – 0.614	-1.021	0.310
Direction [S]	0.782	-1.934 – 0.235	-1.436	0.154
Direction [W]	0.107	-1.441 – 1.162	-0.164	0.870
Female: Route choice	0.369	-1.610 – 2.342	0.369	0.712
Subadult: Route choice	0.890	-2.665 – 0.849	-0.999	0.320
Male: Route choice	NA	NA	NA	NA
Subadult: *Trite*	0.593	-2.846 – 1.510	-0.551	0.583
Male: *Trite*	0.172	-2.196 – 2.481	0.148	0.882
Trite: Route choice	0.458	-1.652 – 2.711	0.425	0.672

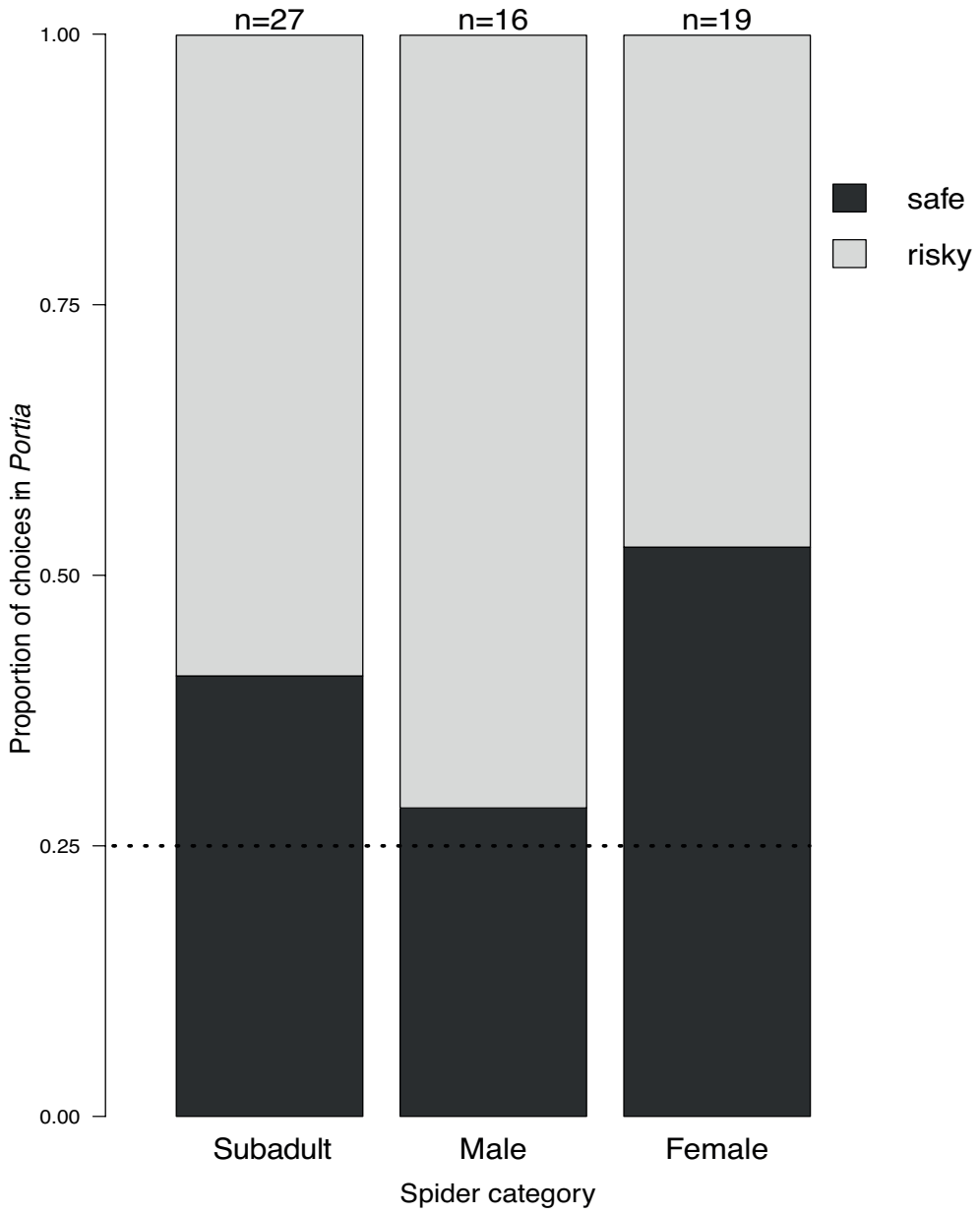

Figure 3. Experiment 1. Proportion of safe escape choices compared with the risky choices for each spider sex/age category in *Portia fimbriata*. Dotted line depicts the proportion of safe choices if spiders performed randomly (25% probability).

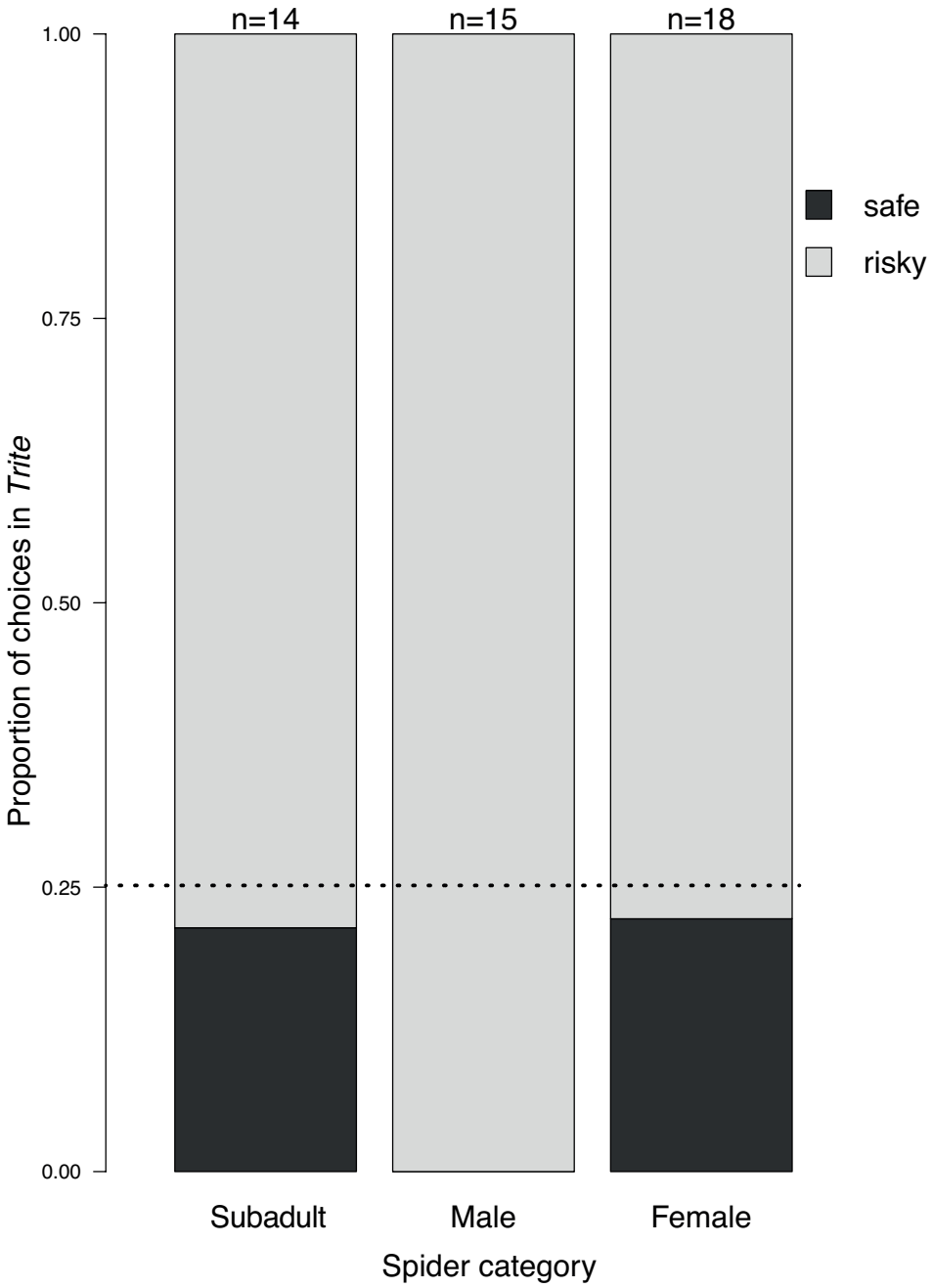

Figure 4. Experiment 1. Proportion of safe escape choices compared with the risky choices for each spider sex/age category in *Trite planiceps*. Dotted line depicts the proportion of safe choices if spiders performed randomly (25% probability).

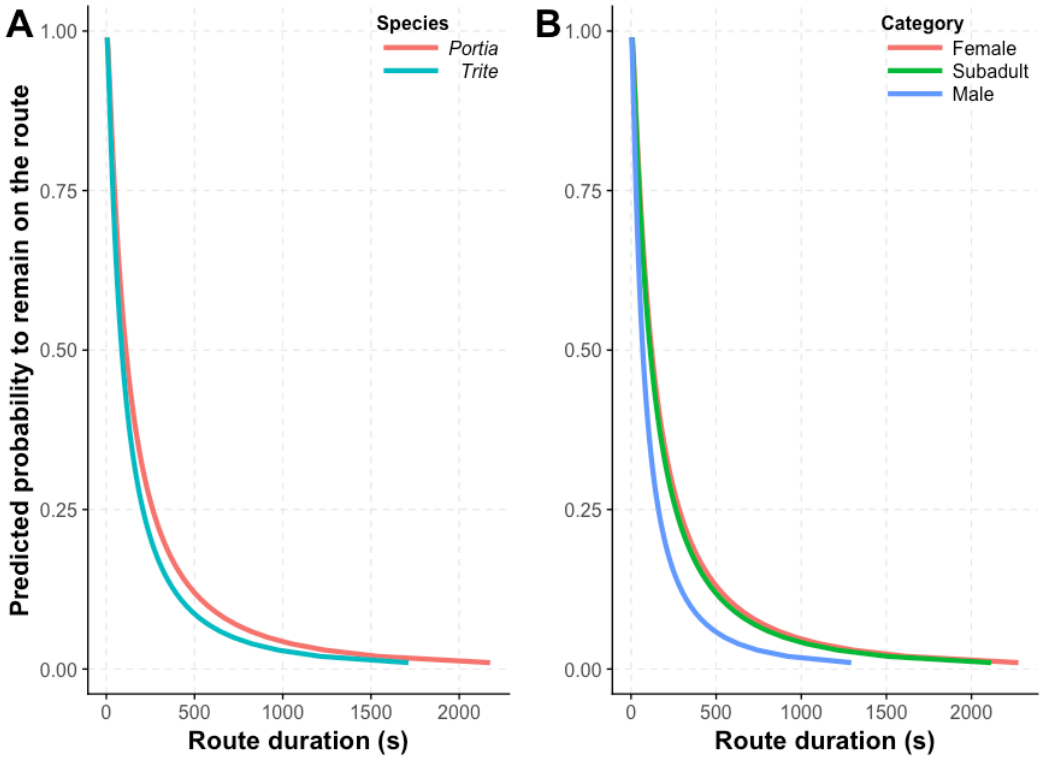

Figure 5. Accelerated Failure Time model curves depicting the probability of continuing to escape using the chosen route over time in Experiment 1 for (**A**) *Portia* and *Trite* spiders and (**B**) sex and age categories of both species combined. *Portia* was more likely to stay *en route* than *Trite*, and females and subadults were more likely to stay on the chosen route than males.

Experiment 2

2.2 Determining route preference for both species

Apart from providing information about the effect of the explanatory variables on route choice, the cumulative link model (CLM) also estimates the coefficient thresholds. These are the intercepts of each chosen route distributed in a cumulative fashion. To calculate the cumulative probability of choosing each route by order of route length (4-dowel, 5-dowel, 6-dowel, and 7-dowel route), we ran different versions of the CLM while re-arranging the levels of the species and spider category variables. Each model calculates threshold coefficients (estimates and standard errors) of a particular species/category combination. After obtaining all values for the three thresholds (4|5, 5|6, and 6|7) in the six different combinations (females, males and subadults for both species), we calculated the inverse variance weighted mean (IVWM) for each threshold belonging to each species (including male, female, and subadult thresholds). We used the IVWM to account for the variance given by the estimated standard errors of each CLM. Finally, the IVWM

was transformed to the inverse logit in order to obtain the probability values of each threshold. Confidence intervals were calculated by using the summary of the inverse variances of female, male and subadult threshold coefficients, and then transformed to the inverse logit (**Table 2**).

Table 2. Cumulative probabilities (*P*) and confidence intervals (CI) of both species and their chosen routes. Values were calculated from ordinal logistic regression models for all data (shortcut-taking and non-shortcut-taking spiders), and separately for non-shortcut-taking spiders. Threshold 4|5 = intercept of using 4-dowel route against 5-dowel route or longer. 5|6 = intercept at choosing either 4 or 5-dowel route against choosing 6 and 7-dowel routes. 6|7 = intercept at choosing 4, 5 or 6-dowel route against using the 7-dowel route.

All data included				
	Portia		*Trite*	
Thresholds	*P*	CI	*P*	CI
4|5	0.348	0.279, 0.425	0.247	0.188, 0.317
5|6	0.555	0.481, 0.628	0.435	0.359, 0.513
6|7	0.688	0.620, 0.749	0.576	0.50, 0.648
Non-shortcut-taking spiders only				
	P	CI	*P*	CI
4|5	0.484	0.364, 0.606	0.342	0.248, 0.450
5|6	0.681	0.566, 0.777	0.542	0.436, 0.644
6|7	0.784	0.683, 0.859	0.667	0.569, 0.753

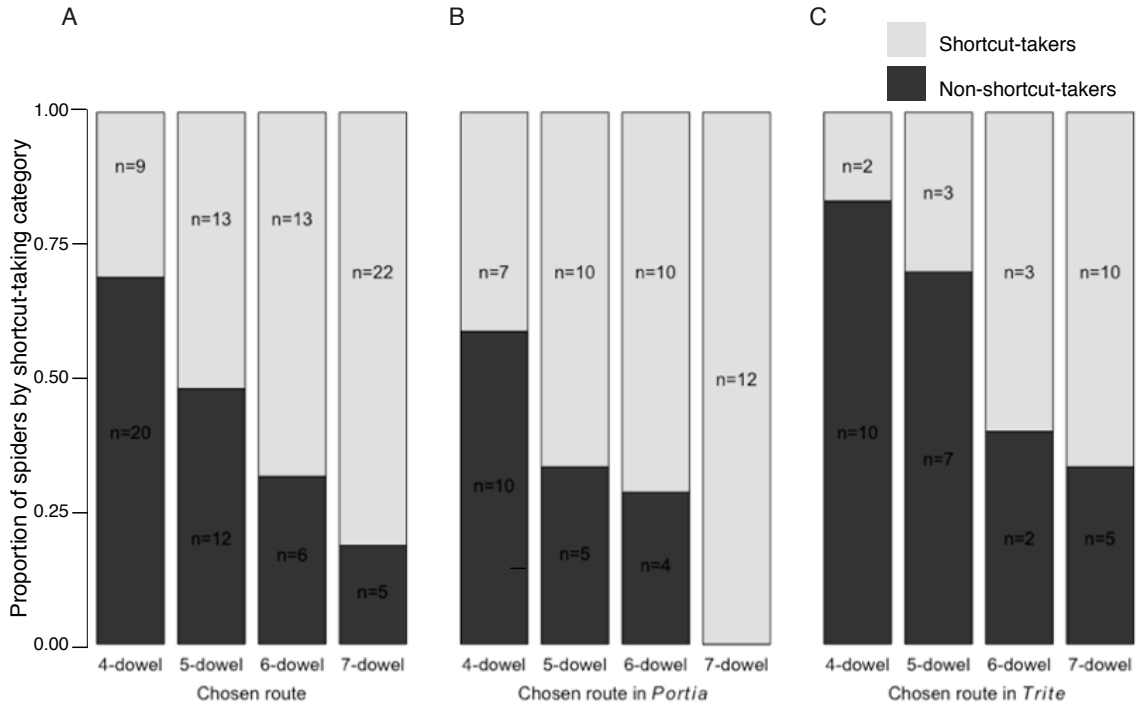

Figure 6. Experiment 2. (**A**) Combined data from *Portia* and *Trite* spiders showing the proportion of individuals that took or did not take shortcuts relative to the total that chose each route. (**B**) Proportion of *Portia* spiders that took shortcuts to different degrees for each chosen route. (**C**) Proportion of *Trite* spiders that took shortcuts to different degrees for each chosen route. Level of shortcut-taking of each spider was classified according to their performance coefficient: non-shortcut-taking spiders: performance coefficient > 0.75; shortcut-taking spiders: performance coefficient ≤ 0.75.

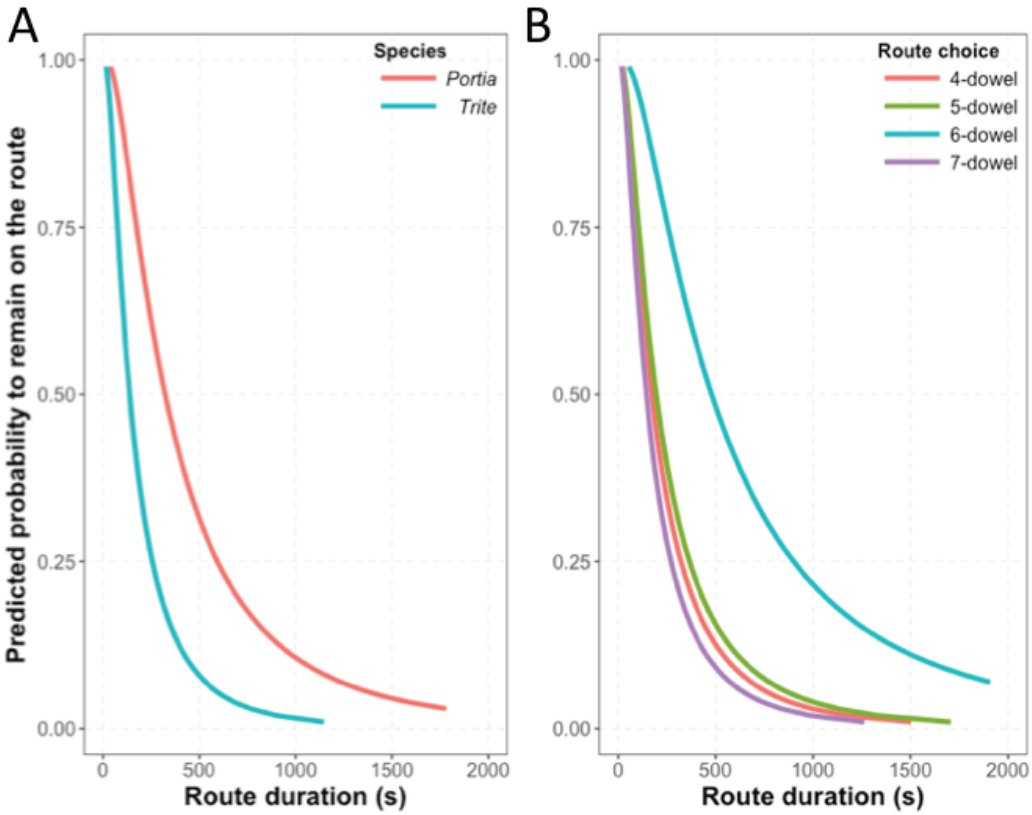

Figure 7. Accelerated Failure Time model curves for non-shortcut-taking in Experiment 2, depicting the probability of continuing on the route chosen over for (**A**) *Portia* and *Trite* and (**B**) routes varying in length for both species combined. In (**A**) two values are removed from the plot for *Portia* as they are higher than 2000 s. In (**B**) six values are removed from the plot in 7-dowel route group. *Portia* were more likely to remain on the chosen route than *Trite*, and route length affected the probability of the spider remaining on that route.

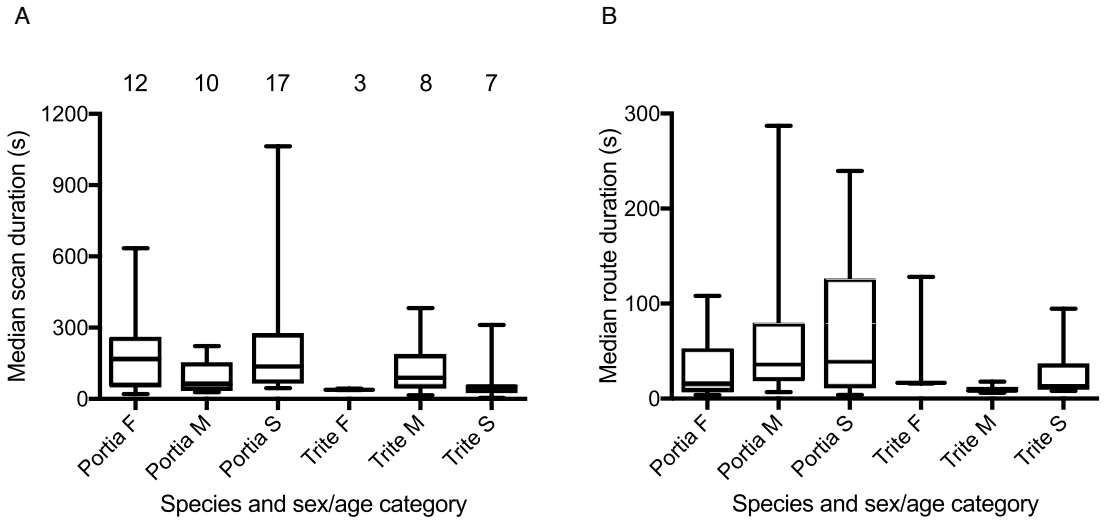

Figure 8. Experiment 2. Comparison of median (box represents 25th and 75th quartiles; whiskers are min to max) (**A**) scanning duration, and (**B**) route duration among the combination of species and spider category sub groups. M = males, F = females, S = subadults. N for each group depicted in (**A**).

APPENDIX 3. Chapter 4

3.1 Control for background noise

To determine if the noise from the leaf blower (experienced in trials with high wind treatment) affected spider behaviour in Experiment 1, we independently tested a separate group of spiders (7 *Portia* and 23 *Trite*) in a further two treatments with the recorded noise of the leaf blower played through a speaker at the same distance from the arena and at same amplitude (82.1 dB) as the leaf blower operating in a high wind trial.

We used a series of GLMs to compare the behaviour exhibited in: 1) no wind control trials with and without added leaf blower noise (i.e., high-noise-control trials, no-noise control trials; the latter group being the spiders tested in Experiment 1), and 2) low wind trials with and without added leaf blower noise (i.e., high-noise-wind trials, low-noise-wind trials; the latter group being the spiders tested in Experiment 1). Note that one *Portia* could not be tested in a no wind control trial (N=7, n=13).

Spider horizontal adjustment did not change depending on added noise (no wind control: estimate = -0.238, CI = -1.378 to 0.901, t = -0.410, P = 0.683; wind: estimate = 0.042, CI =-1.393 to 1.478, t = 0.058, P = 0.954; **Figure 1**). However, in the no wind control trials, spiders jumped at an angle away from the speakers with the presence of added noise, but towards the speakers without background sound (estimate = 10.686, CI = 1.611 to 19.759, t = 2.308, P = 0.024; **Figure 2**); this effect was not evident in the wind trials (estimate 2.898, CI =-6.749 to 12.545, t = 0.589, P = 0.558). Scanning duration was not affected by added noise (no wind control: estimate = 1.094, CI = 0.722 to 1.659, t = 0.425, P = 0.672; wind: estimate = 0.848, CI = 0.556 to 1.292, t = -0.767, P = 0.446). However, in wind trials (estimate =0.588, CI = 0.359 to 0.962, t = -2.111, P = 0.038), but not in no wind control trials (estimate = 0.686, CI = 0.405 to 1.159, t = -1.407, P = 0.164), spiders fixated for longer without added noise (**Figure 3**).

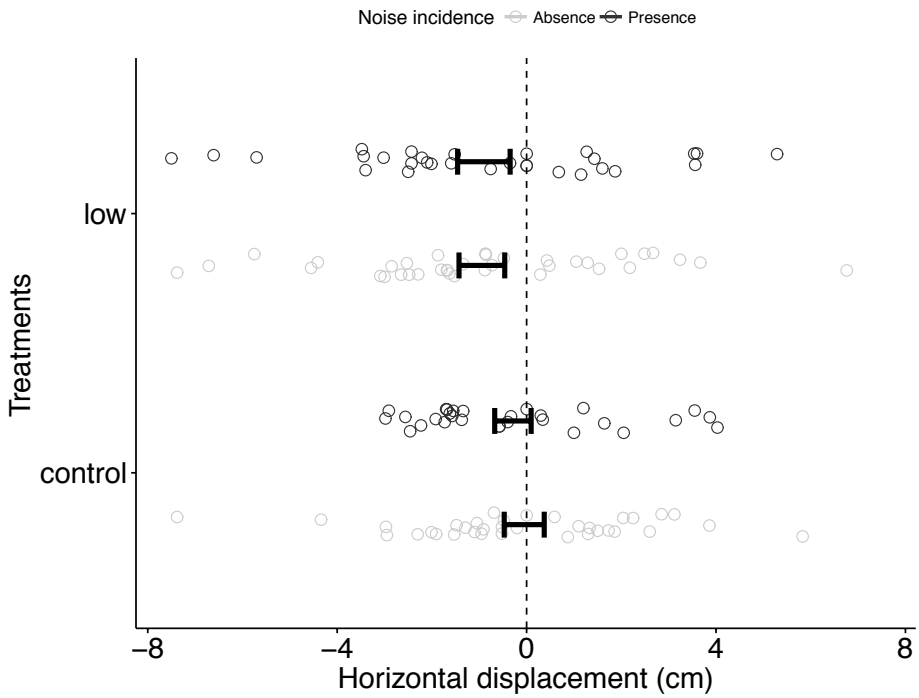

Figure 1. Horizontal displacement (±SEM) of spiders prior to jumping when exposed to different low wind and no-wind control treatments with (dark circles) and without (light circles) added noise. Data are presented such that wind direction is depicted from left to right. Note slight upwind displacement with wind.

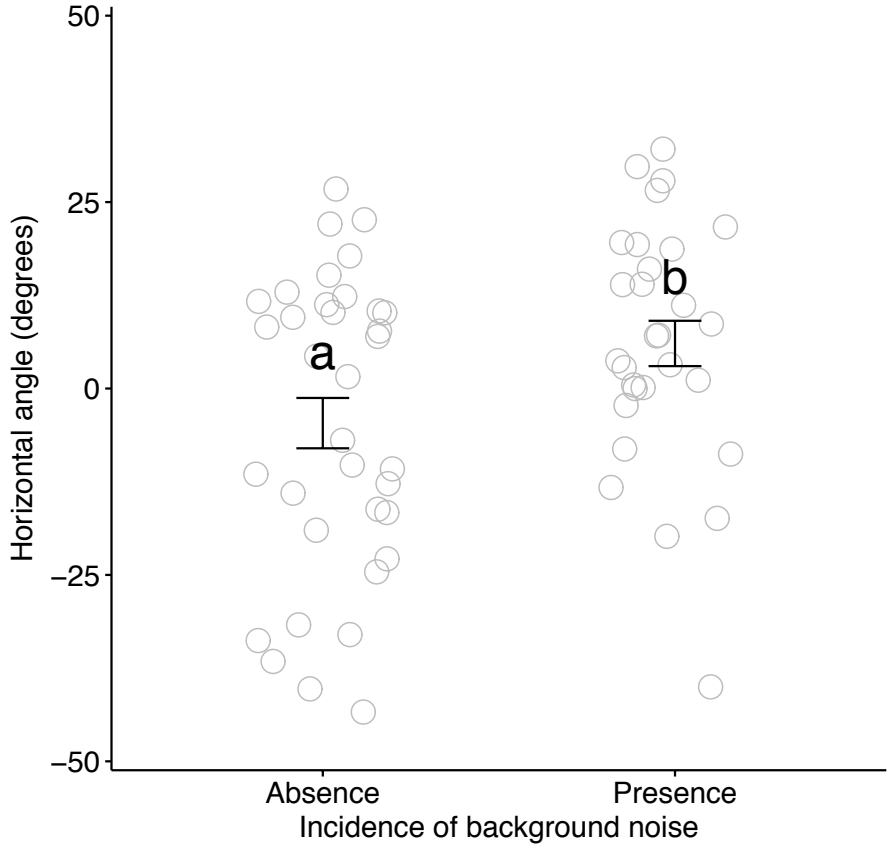

Figure 2. Effect of background noise on the horizontal angle (±SEM) of spiders before jumping during noise-control trials (no wind). Letters denote significant differences between groups. Positive values represent a jump directed away from the noise source (speaker).

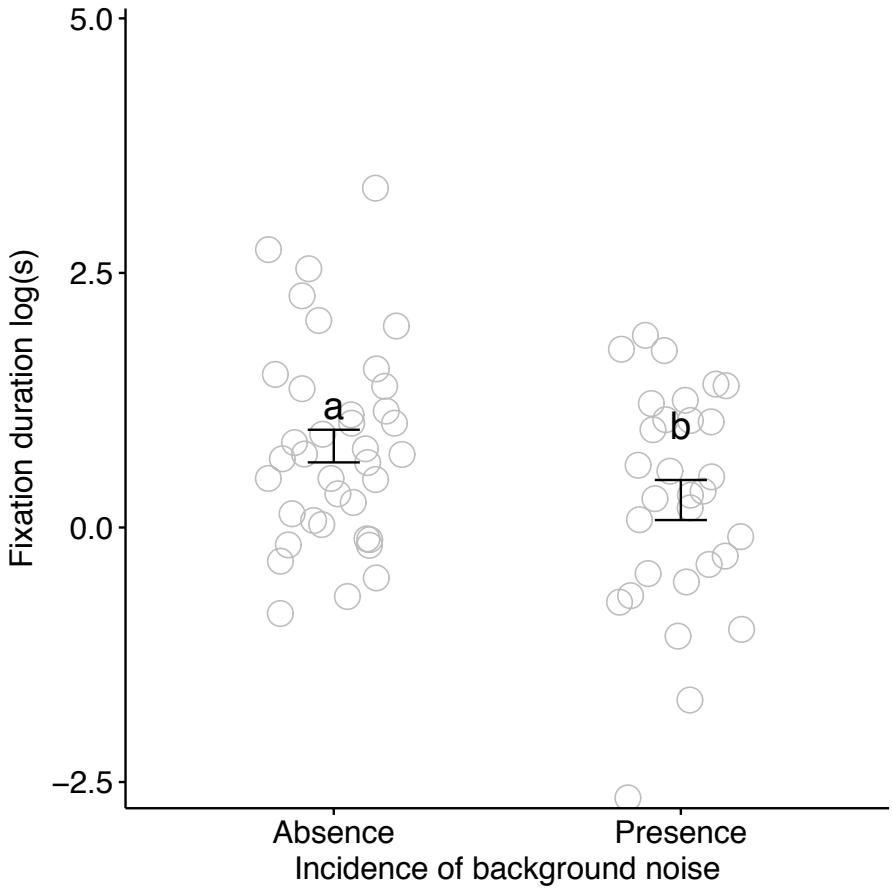

Figure 3. Effect of the background noise on fixation duration (±SEM) during wind trials. Letters denote significant differences between groups.

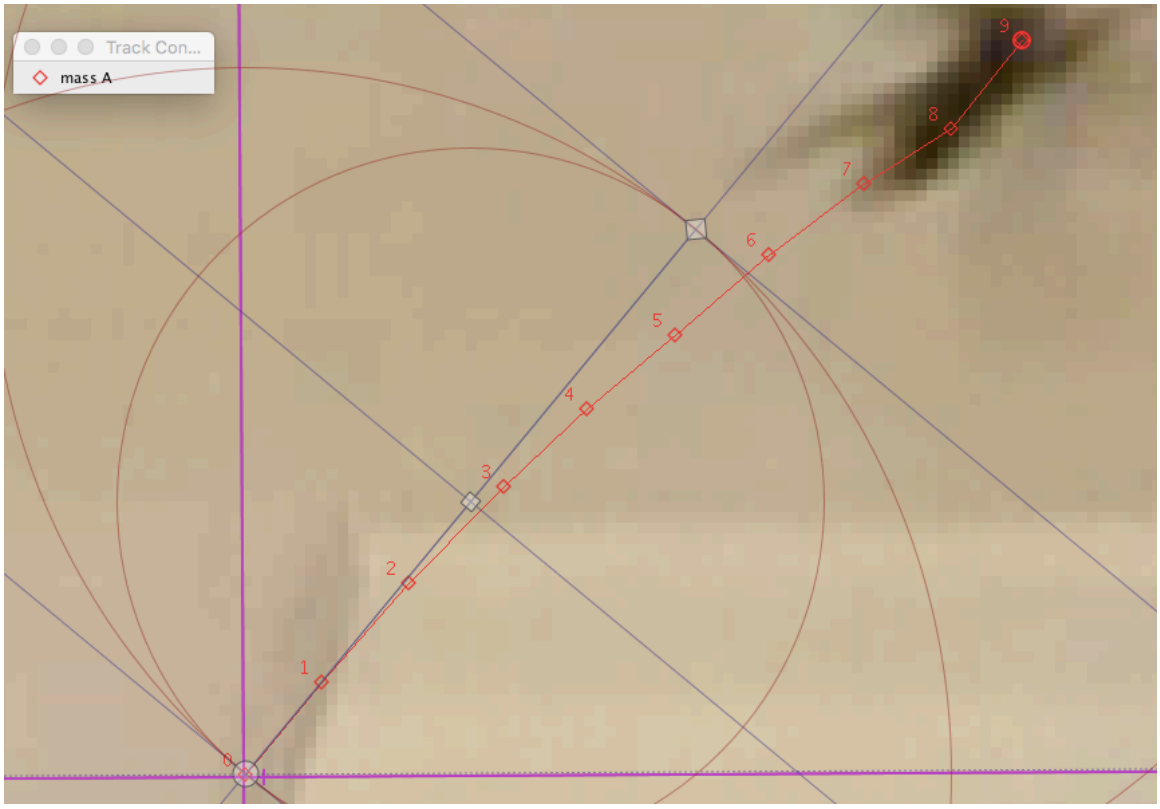

Figure 4. Vertical body angle measurements. Purple lines: reference frame for the origin of x and y axes. Red line: jump trajectory from the start (at the intercept at point 0) to the highest point of the jump (here, point 9). Vertical body angle is the tilt angle of the line connecting points 0 and 1. Measurements were made using Tracker v. 5.0.7 to outline the jump trajectory and PixelStick v. 2.15.0 to measure the angle in degrees. Note: spider is at top right corner.

APPENDIX 4. Published version of Chapters 2 and 3

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Article

Article

Distance assessment of detours by jumping spiders

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Abstract

To take an indirect route (detour) in order to reach a specific target requires complex cognitive processes. Yet more demanding, from the cognitive point of view, is when the goal is only visible at the beginning of the detour. In spiders from the family Salticidae, vision is a key sensory modality mediating navigation and prey search. Their acute vision allows them to perform complicated detours, possibly as a consequence of the multitude of potential routes in their typically complex 3-dimensional habitats. We used a 4-route choice test, in which routes differed in being either short or long and in the presence or absence of a lure of a prey item, to investigate route assessment in 2 salticid species, *Trite planiceps* and *Marpissa marina*. Although both species showed evidence of motivation to follow lured-routes, judging by the number of times they re-oriented toward them while detouring, we found that *Trite* chose short routes in preference to long routes, but did not prefer the lured-routes. In contrast, *Marpissa* exhibited random route choice, although it oriented toward lured-routes more often than control routes (lure absent). Our results suggest that decision-making processes about which route to take occurs before embarking on a route, but this is cognitively challenging. Spiders exhibited cognitive limitations in which the lack of visibility of the goal affected success. However, the severity of cognitive limitations depended on species. We suggest that variability in spatial ability across the Salticidae may be related to the habitat complexity inhabited by each species.

Key words: cognition, cognitive limitations, decision-making, detour behavior, Salticidae, spatial task

The cognitively simple process of moving in a straight line toward a visualized goal occurs as an instinctive response (Köhler 1927). However, using an indirect route to reach a goal (detouring) requires mental operations beyond innate responses, such as different types of learning and disruption/retention mechanisms (Kabadayi et al. 2018). Even more complexity is required when the goal becomes invisible while the individual executes the detour. In this case, without the use of cues emanating from the goal, the subjects rely on working memory, route planning, and orientation (Wells 1967; Cross and Jackson 2016). The latter detours can be performed by vertebrates (Regolin et al. 1995; Zucca et al. 2005), and also by invertebrates with outstanding eyesight, such as octopuses (Wells 1970) and jumping spiders (Araneae: Salticidae) (Cross and Jackson 2016). Salticids are characterized by their highly acute vision (Land 1969; Harland et al. 2011) based on a visual system comprised of one pair of principal eyes and 3 pairs of secondary eyes. The principal, or anterior medial eyes (AMEs), are crucial for high spatial acuity and color vision, whereas the secondary eyes can detect motion over about 360° surrounding the spider (Harland et al. 2011).

In salticids, vision is a key sensory modality mediating prey capture (Jackson 2000; Li et al. 2003), agonistic displays (Wells 1988; Taylor et al. 2001), visual courtship (Clark and Morjan 2001), and navigation (Hoefler and Jakob 2006). When foraging, salticids visually identify their prey at a distance (Richman and Jackson 1992)

and stalk prey using a readily observable set of behaviors: the spider initially orients its cephalothorax toward the prey with the AME facing it—a behavior known as "orientation," after which, if prey is identified, the salticid slowly approaches and finally catches it by pouncing from 2 to 3 cm (Forster 1977). When a direct route to reach a visually located prey is not available, salticids may perform detours (Punzo 2004; Jakob et al. 2011). Detouring implies route planning (Cheng 2016) and spatial learning or ability (Thorpe 1963; Healy 1995). Scanning behavior, in which salticids systematically move their cephalothorax and body to inspect their surroundings using their AME, precedes detours, and is believed to be crucial for a priori-based route selection (Tarsitano and Andrew 1999; Cross and Jackson 2016). However, while detouring, salticids may not always see the goal, and may rely on spatial memory or on an internal representation of the prey's relative position (Hill 1979; Tarsitano and Jackson 1992; Tarsitano and Andrew 1999; Tarsitano 2006). During a detour, salticids often "re-orient" toward the location of the goal in order to keep track of it (Hill 1979). Such re-orientations allow the spider to readjust its detour or stop detouring if the goal (e.g., prey) moves to another location. Detours are represented by a sub-goal (e.g., leaf or branch), or a series of sub-goals, that spiders need to initially reach to enable access to the main goal. Hence, using detours implies making associations of sub-goals that will lead to the primary objective. Hill (2007) suggested that salticids can use tertiary and possibly quaternary objectives depending on the length and complexity of the detour.

Commonly living in complex 3-dimensional environments, salticids are likely to encounter several possible detours that may or may not lead to a desired goal. Thus, decision-making becomes essential from an adaptive point of view (Punzo 2000), as choosing the most efficient route (the one that leads to prey, the shortest, the safest, etc.) allows the spider to save time and energy, and to be less vulnerable to predators (Gibson et al. 2007). Several salticid species have been shown to take detours (Hill 1979; Tarsitano and Jackson 1992, 1994; Carducci and Jakob 2000; Cross and Jackson 2016), suggesting this to be a common behavior in this family. Previous studies about detour assessment in salticids have focused on testing spatial abilities of species in the subfamily Spartaeinae (Jackson and Wilcox 1993; Tarsitano and Jackson 1994), and the majority of these studies provide 2 alternate detours (one detour leading to prey and a no-prey control; Tarsitano and Jackson 1992, 1997; Tarsitano 2006; Cross and Jackson 2016). However, detour assessment combining length and the presence of prey as factors has not yet been tested. We tested this using a 4-choice test with 2 long and 2 short routes, with a prey lure on one of the long and on one of the short routes. Using 2 species of salticids from the Salticoida subgroup, *Marpissa marina* Goyen and *Trite planiceps* Simon, we wanted to determine: (1) if salticids are able to decide on a route during the scanning phase before embarking on a route, and remember this even after the goal is visually blocked; (2) if salticids prefer short routes over long routes; and (3) if there are species-specific differences in spatial ability.

As salticids can follow a secondary objective while apparently memorizing the spatial location of the goal (Hill 1979), we predicted that the spiders would reach the goal even if they could only see it at the beginning of the task. We also expected that salticids would choose the short route leading to prey compared with the other 3 routes; this being the most efficient route to a goal. It is known that closely related species can differ in spatial ability as a consequence of the environment in which they live (Kasumovic et al. 2013) because the environment can directly affect cognitive (van Praag et al. 2000) and spatial abilities (Parker and Gibson 1977; Striedter 2005; Park and Bell 2010). Consequently, we expected *Trite* to outperform *Marpissa*, because it inhabits a 3-dimensionally more complex habitat.

Materials and Methods

Test animals

All animals were collected in Canterbury, New Zealand. Experiments were carried out from 08:00 to 13:00 h in the laboratory at the University of Canterbury. *Trite planiceps* is a large (6–13 mm) salticid endemic to New Zealand and is typically found in coastal areas where it inhabits the rolled-up flax leaves of *Phormium tenax* and *Cordyline* spp. (Forster 1979). *Trite* were field-collected in Christchurch and were transferred to the laboratory, where they were housed individually in 1-L transparent plastic containers. Individuals were held in captivity for at least 1 week before testing. Water supply was available through a cotton wick submerged in water which protruded into the container. Spiders were fed weekly with 2 adult *Musca domestica*. Hunger level during testing was standardized by performing the tests 5–7 days after their previous meal, thus ensuring similar hunger levels between individuals.

Marpissa marina is native to the South Island of New Zealand. It lives in quite flat rocky shores and makes nests 2–6 m above the high tide mark (Vink and McQuillan 2015). Adult males are 5–8 mm and females 6–9 mm in body length, and subadults are typically about 1 mm smaller than adults. Collected individuals were housed and maintained as described for *Trite*.

Experimental setup

We exposed spiders to 4 different routes from which to choose in order to reach a prey (i.e., lure made from a dead fly on the goal platform, described below). To determine if spiders were able to evaluate, or cared about, the distance of the route to reach a prey, the routes were either long or short. Additionally, to identify if spiders were actually following a route because of the prey rather than as a consequence of random choice, the goal platforms at the end of each route either did, or did not, have prey. Thus, the 4 different routes were: (1) short-lured route; (2) long-lured route; (3) short-control route; (4) long-control route. We tested 53 *Trite* (23 females, 16 males, and 14 subadults) and 63 *Marpissa* (25 females, 19 males, and 19 subadults).

The arena (see Figure 1 for dimensions) consisted of an aluminum tray with a central starting platform (a wooden dowel) on which the spider was placed at the beginning of every trial. Surrounding the starting platform there were 4 routes made of articulated plastic sections (each 2.5 cm long) with magnetic bases. Short routes had 10 articulated sections (25 cm) and the long routes had 22 sections (55 cm). The distance from the starting platform to the goal platform on a long route was 114 cm, and 84 cm for short routes. All goal platforms were at the same height (20 cm) and distance (17 cm) from the starting platform, with the route bases being 30 cm from the base of the starting platform. Consequently, the spider could see the 4 goal platforms at the same distance and height from the starting platform. External visual cues were blocked by black screens and the corner wall of the laboratory.

Goal platforms consisted of a square plate (4 × 4 cm) of aluminum with an attached "jiggler." The jiggler allowed 5 Hz movement of a rigid wire (15° to each side of the vertical for 2 s; Dolev and

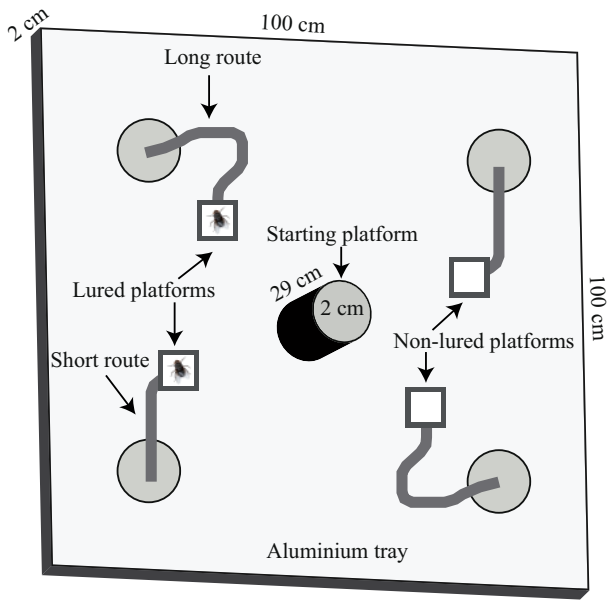

Figure 1. Aerial view of experimental arena (not to scale). To begin a test, spiders were placed on the starting platform from which they observed the 4 different routes to goal platforms with or without dead prey (lures).

Nelson 2016) to simulate prey movement when a lure was stuck on the wire. In control route goal platforms, this was comprised by the wire and a thin (1 mm) disc of cork, while in prey goal platforms, a dead prey on a thin cork disc was attached to the wire. Lures were adults of *Musca domestica* attached to the cork disc in a lifelike position and covered with transparent aerosol plastic adhesive (Jackson and Cross 2015). Jiggler movement, which serves to maintain the spider's attention, was activated only when the spider was facing a goal platform and any movement was stopped when the spider left the starting platform.

Spiders were placed on the starting platform in the center of the arena to begin a test. This allowed them to visually scan their surroundings to identify a goal, as once the spiders left the starting platform toward the base of the arena, visual cues on the goal platforms were no longer visible to test spiders. To eliminate directional bias, we randomly rotated the arena in 1 of 4 locations (North, South, East, and West). The position of the lures with respect to the routes (lure configuration) was also randomized for every trial. Consequently, each spider was exposed to one cardinal location plus one lure configuration. Each trial lasted 20 min, or less if the spider reached the lure; exceptions occurred when 20 min elapsed but the spider had started climbing one route. In these cases, trials ran until the salticid reached the end of the route or until it jumped off the route. However, if 20 min had elapsed and spiders had not left the starting platform or if the spider reached the edge of the arena, the spider was re-tested the next day. The arena was wiped with 80% ethanol between tests.

Analyses

Each trial was recorded with a Logitech c920 HD Pro webcam placed 40 cm above the arena. In our analyses we accounted for spider species and age/sex category (adult male, adult female, subadult). From our footage we scored "initial heading," defined as the final orientation toward any of the 4 goal platforms just before approach (either by walking or jumping toward it), suggesting initial route preference (Tarsitano 2006). As the initial heading did not always coincide with the final chosen route, these data were qualified with "decided" if the initial heading coincided with the chosen route, or "undecided" if it changed. When spiders did not exhibit an initial heading, this was scored as N/A. We also scored the frequency of orientations during the scanning phase (i.e., a turn of the cephalothorax toward the goal platform while the spider was at the starting platform). The number of re-orientations during the detour were also recorded (see Supplementary Methods). Additionally, we measured "scanning duration" as the elapsed time from when the spider started scanning until it left the starting platform, as well as the time from the end of scanning phase to the end of the trial ("route duration"), the chosen route, the cardinal "direction" of the chosen route, and the position within the route at which the spider abandoned the route, or "giving up point" (Tarsitano and Jackson 1997). This was divided into 4 sections: (1) passing the magnetic base of the chosen route base but advancing no further; (2) climbing no more than half-way up the route; (3) reaching the second half of the route; and (4) reaching the goal platform or the last plastic articulation of the route (2.5 cm before the platform).

All analyses were done using R v.3.3.3 (R Development Core Team 2018). To determine route preferences, we performed 2 comparisons of multinomial probabilities for count data for each species. We calculated simultaneous confidence intervals (CIs) for the comparison of multiple odds between multiple multinomial samples (following Schaarschmidt et al. 2017) using the "multcomp" (Hothorn et al. 2008) and "nnet" (Venables and Ripley 2002) packages. We excluded highly influential data (outliers) from the model with a Cook's distance value (which combines the leverage and residuals of each data point) > 0.5 (Crawley 2007). The first analysis compared the probability of choosing a specific route (the route with the highest probability to be chosen) with the probability to choose the other 3 routes separately. Here, the baseline was the route with the highest probability of being chosen (short-lured route for *Trite*; long-lured for *Marpissa*). The second analysis compared the probabilities to choose either long or short routes, and either control or lured routes, plus their interactions (see Schaarschmidt et al. 2017).

To identify if spiders followed a specific route as a consequence of decision-making while on the starting platform and not by choices made after leaving the platform, we analyzed the final choice with respect to the initial heading for each species. Data from spiders that did not orient to any route before leaving the starting platform (N/A) were omitted. Here, we used a comparison of multinomial probabilities (for count data) to determine if the probability of a route being chosen depended on its congruence with the initial heading (i.e., "decided" spiders). Here we used 95% CIs, calculated using both Dirichlet (DP) and Wald methods. In these cases, a P value < 0.05 is found when "1" is contained within the CI for the odds ratio between decided and undecided spiders, such that the hypothesis that the groups are not different is rejected (Schaarschmidt et al. 2017).

Initial choice may not concur with the chosen route because spiders may not choose based on the last orientation toward a route before leaving the starting platform, but instead may survey the possible alternatives during the entire scanning phase. Consequently, the number of orientations during the scanning phase may be a better indicator of an association between the targeted route at the starting platform, and the chosen route at the end. In this case, we predicted that spiders that associate the correct route to their final goal (which we expected to be lured-routes, especially short ones)

would have a higher number of orientations during scanning. To determine this, we performed a GLM with a Poisson distribution with the number of orientations as the response variable. Spider category and chosen route were used as explanatory variables in the model for *Trite*, all of which completed routes. For *Marpissa*, we omitted 3 outliers (values: 14, 16, and 20 orientations). This model accounted for spider category, chosen route, and giving up point as explanatory variables, as several *Marpissa* did not complete routes. Contrast tests were then applied with the "gmodels" package (Warnes et al. 2015). Additionally, to determine whether the completion of the route (as a binary variable) depended on the number of goal orientations in *Marpissa*, we analyzed the data with a binary logistic regression, with completion of the route (0 = incomplete routes, 1 = completed routes) as the response variable and the number of goal orientations as the independent variable (Crawley 2007); we omitted one outlier for this analysis.

To investigate species-specific differences, we used the general dataset (this includes trials in which the individual chose a route irrespective of whether it was completed). Here, we performed a comparison of multinomial probabilities for count data, using the 4 routes as the categories (chosen route) and species as the treatment groups. The first analysis compared the baseline (short-lured) route with the other 3 routes. The second analysis was a specific comparison using the Wald and DP methods. The latter compared the probability to choose either control routes and lured routes, or short routes and long routes. To determine whether the number of orientations differed between species, we performed a GLM with a Poisson distribution, omitting N/A's and excluding outliers from 3 *Marpissa* individuals. Orientations were the response variable and species the explanatory variable. We used the same analysis, using data from completed routes only, to explore differences in the number of re-orientations (see Supplementary Methods).

We analyzed scanning duration and route duration using accelerated failure time regression (AFT) survival models, allowing us to compare the hazard function, or the risk of an event to finish, and a set of explanatory variables. Each AFT model was selected based on the distribution with the minimum AIC value, which exhibited the best fit to the data (Cox 1972). Second-order interactions among the explanatory variables were not accounted for, as the AIC value for the full model was higher than the selected model. Scanning duration was set as the response variable, with species, chosen route, and spider category as explanatory variables. With this configuration, we ran 2 AFT models using different datasets: the first model (Weibull distribution) used the general dataset, while the second used the subset of spiders that completed a route ("giving up point" = 4); in this model a log-logistic distribution was selected to better fit the data.

For route duration, the selected AFT model accounted for route duration as the response variable and species, spider category, and chosen route as the explanatory variables. Based on the AIC value, the best-fit error distribution for the general dataset was log-logistic. Additionally, we ran survival analyses using individuals that completed the route only; therefore, all 53 *Trite* individuals were included in the model, but only 25 *Marpissa*. Model selection was performed under the step model and here the best-fit error distribution was lognormal.

Results

For those spiders that made a choice, the log-odds between decided and undecided spiders did not differ between routes, either for *Trite* or *Marpissa* (Figure 2, Table 1, and Supplementary Table S1 for probabilities). Additionally, when comparing control and lured-route choices, we found no difference in odds-ratio between decided and undecided *Trite* (95% CI for odds-ratio: DP method: lower = 0.35, upper = 12.01, Wald method: lower = 0.29, upper = 15.95) or *Marpissa* (95% CI for odds-ratio: DP method: 0.80, 15.16, Wald method: 0.75, 20.51), nor were there differences between long and short routes (*Trite*: DP method: 0.17, 5.47, Wald method: 0.13, 6.98; *Marpissa*: DP method: 0.10, 1.86, Wald method: 0.07, 1.99).

The number of orientations toward the chosen route was higher (estimate = 0.4908, $Z = 4.186$, $P < 0.0001$) in *Trite* (mean ± SEM; 3.32 ± 0.45) than *Marpissa* (2.03 ± 0.32). *Trite* which chose the short-control route made significantly less orientations (Figure 3A) compared with the other 3 routes, and subadults oriented more than females and males (Figure 3B and Supplementary Table S2). In contrast, in *Marpissa*, the number of orientations was not influenced by chosen route or spider category, but was significantly higher among spiders that completed all 4 sections of the route, rather than those that gave up early (Figure 3C and Supplementary Table S3; note that no *Trite* gave up early). This was confirmed using a binary logistic regression which showed that *Marpissa*'s probability to complete routes was related to the number of goal orientations (95% CI = 0.029–0.509, Estimate = 0.2699, $Z = 2.203$, $P = 0.027$; Supplementary Figure S1). Similar trends were found with the number of re-orientations (Supplementary Figures S2, S3 and Supplementary Tables S4, S5).

In *Trite*, the probability to choose lured, compared with control, routes did not differ and there was no interaction between lure presence and route length (Table 2). Although the probability to choose the short-lured and short-control routes did not differ, *Trite* was more likely to choose short routes (Figure 4). In *Marpissa*, there were no differences in the probabilities to choose any route, nor were there any interactions, both among spiders that completed routes, and all spiders from the general dataset (Table 2). When comparing the general dataset for both species, the log-odds between choosing long-control with respect to short-lured routes and choosing long-lured compared with short-lured routes were significantly higher in *Marpissa* than *Trite* (Table 3). However, the odds ratio of choosing short-control with respect to short-lured routes did not differ between species (Figure 5). The odds ratio of choosing long routes with respect to short routes was significantly higher in *Marpissa* (95% CI for odds-ratio: DP method: lower = 2.05, upper = 15.98, Wald method: lower = 2.04, upper = 18.82). However, the odds ratio between control and lured routes did not differ between species (95% CI for odds-ratio: DP method: lower = 0.53, upper = 15.98, Wald method: lower = 0.51, upper = 4.70).

Across all spiders, the probability to remain at the starting platform scanning the surroundings (scanning duration) was not significantly affected by the chosen route (Supplementary Table S6). Nevertheless, there were species-specific behavioral differences, with *Marpissa* scanning for longer than *Trite* (max: *Trite* 966 s, *Marpissa* 1934 s; $P_1 = 0.016$; Figure 6A). Additionally, females scanned for longer than subadults (Figure 6B). The same effects were found when considering only individuals that completed a route (Figure 6C, D). The time to reach the giving up point was also unaffected by species, spider category, or by chosen route. However, route duration was lower in males than females, both for all spiders (Figure 7A and Supplementary Table S7) and among spiders that completed a route

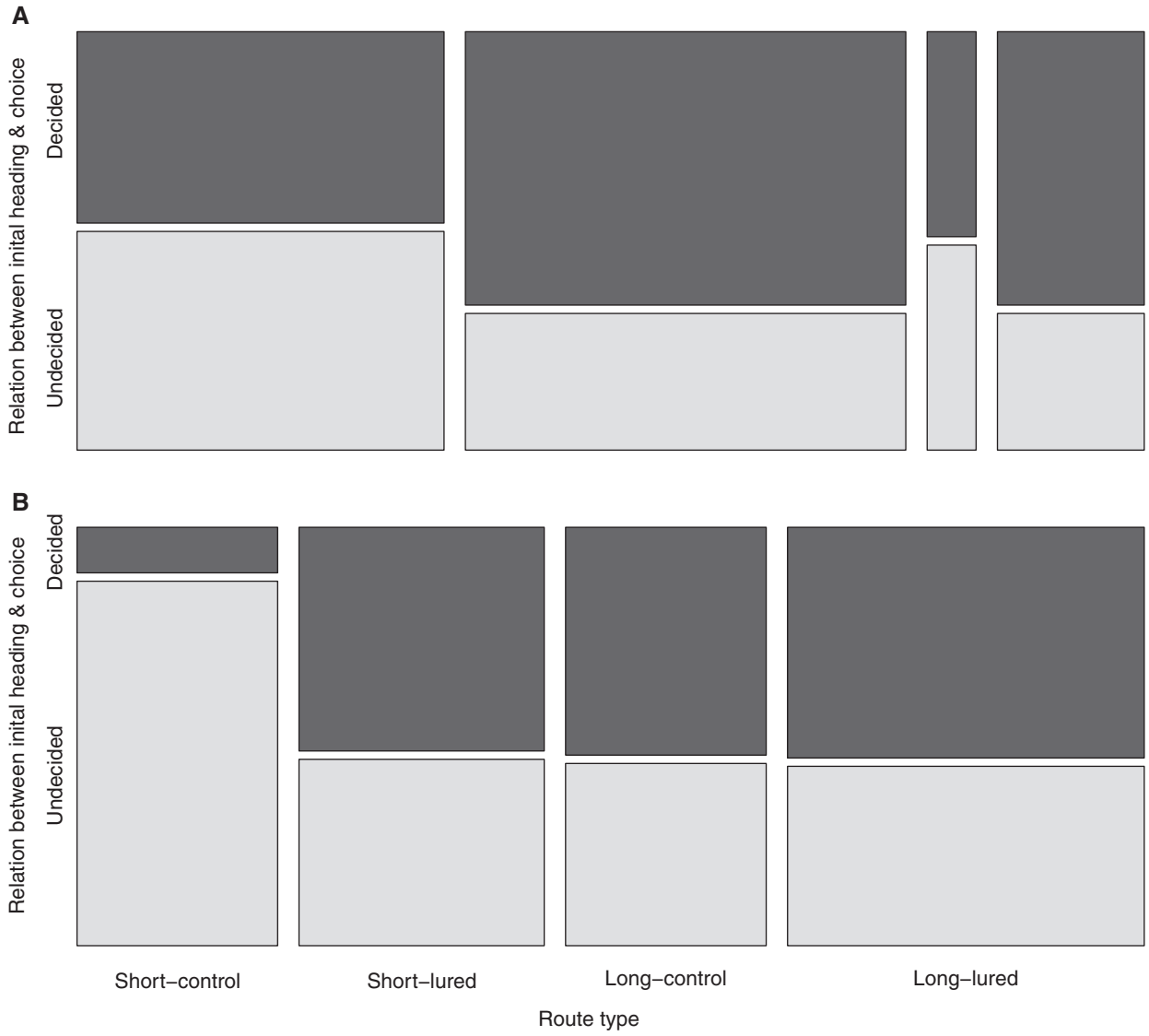

Figure 2. Mosaicplot showing the proportions of (**A**) *Trite* and (**B**) *Marpissa* spiders that did not change (decided) and those that changed their choice (undecided) for the 4 routes. Horizontal axis depicts the proportion of total spiders tested that used a given route type. Vertical axis depicts the proportion of total spiders tested that were decided or undecided for each given route type. The total area of each shaded section depicts the combined proportion of the given variables.

Table 1. Comparison of multinomial probabilities for number of decided/undecided spiders between the short control route and the other 3 routes chosen by *Trite* and *Marpissa*

Trite				
Comparisons between route variables (decided/undecided)	Estimate (odds-ratio)	SEM	*Z*	*P*
Short-lured/short-control	0.826	0.719	−1.149	0.561
Long-control/short-control	0.135	1.506	−0.089	1
Long-lured/short-control	0.826	1.008	−0.89	0.783
Marpissa				
Short-lured/short-control	2.262	1.221	−1.852	0.129
Long-control/short-control	1.856	1.255	−1.479	0.26
Long-lured/short-control	2.33	1.174	−1.985	0.097

(Figure 7B). In the latter subset, *Trite* was faster than *Marpissa*, Figure 7C) and spiders that chose long routes took longer than those choosing short routes (Figure 7D and Supplementary Table S8).

Discussion

This study provides evidence of cognitive limitations while performing spatial tasks in 2 salticid species, contributing to a broader view of the differences of spatial ability within the Salticidae. In

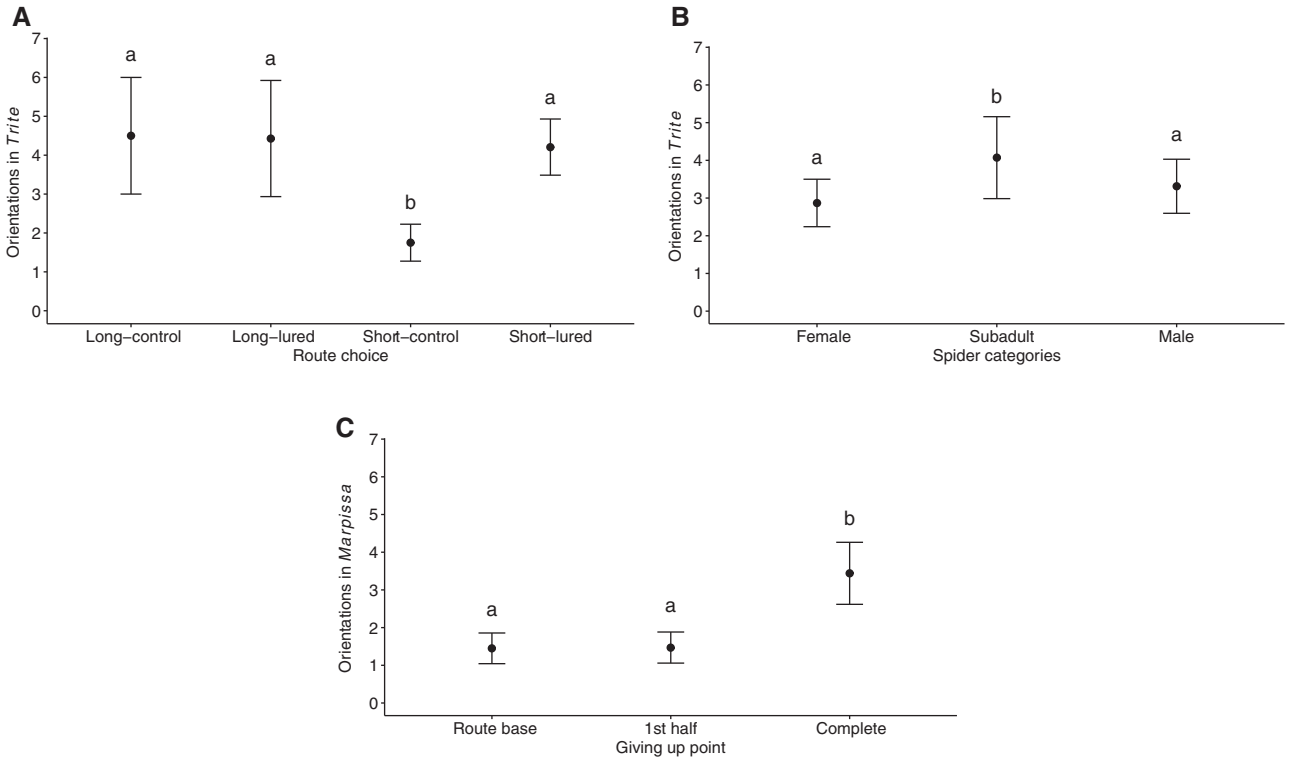

Figure 3. Mean (±SEM) number of orientations by (**A**) chosen route in *Trite*, (**B**) *Trite* spider category, and (C) giving up point in *Marpissa*. Letters indicate significant differences between groups.

comparison with previous studies, our detouring tasks were especially complex (4 choices varying in length and presence of prey and in which visual access to prey was denied after leaving the starting platform). Nevertheless, we found evidence that spiders are able to make decisions while on the starting platform before embarking on a route, and we also observed interspecific differences in route-choice behavior. While we anticipated that the short-lured route would be preferred, due to being more efficient (shorter) and containing prey, spiders did not exhibit this preference. *Trite* did prefer short over long routes, but showed no preference for lured routes, possibly because the task was too cognitively demanding. In *Marpissa*, spiders showed no route preference, and may have chosen routes randomly. However, arguing against this, in their frequency of orientations and re-orientations, *Marpissa* demonstrated some evidence that they can discriminate lured from control routes.

Route choice did not affect scanning or route duration for either species, but *Trite* completed routes faster than *Marpissa*, which may have struggled more to solve the task than *Trite*: although *Marpissa* spent more time scanning, the number of orientations was lower than *Trite*'s, and *Marpissa* only completed routes when they frequently oriented (and re-oriented) toward the goal platform. Indeed, compared with the salticid *Portia*, *Trite*'s fast performance in spatial tasks previously suggested to us that *Trite* faces a trade-off between fast route completion but deficient route assessment (Aguilar-Arguello et al. 2019). We cannot discard that previous experience with houseflies in nature may have caused different behaviors between species, as we have little information about housefly availability in their natural habitats, other than they exist in both habitats. However, for decades houseflies have been used as standard prey for predator-related experiments for both of these species (e.g., Forster 1977, 1979; Tarsitano and Jackson 1992; Jackson and Tarsitano 1993), confirming that houseflies are attractive prey. We also found that spider categories behaved similarly across species, with subadults finishing the scanning phase faster. As it is known that adults are more capable at solving learning tasks than juveniles (Edwards and Jackson 1994; Skow and Jakob 2005; Hill 2006), this suggests that they may require experience to develop attentional skills for spatial tasks. Spiders are strongly influenced by innate behavior; however, cognitive skills are flexible enough for innate behaviors to be perfected (Forster 1977; Edwards and Jackson 1994; Bartos and Szczepko 2012). Thus, it is reasonable to expect better performance in adults than in subadults, but, unfortunately, few performance differences were observed. Nevertheless, males completed routes faster than subadults and females. The speed at which males completed routes was surprising, as previous work indicates that females are more motivated than males in predation-based (Jackson and Wilcox 1990) or learning (reviewed in Jakob and Long 2016) tasks. Because of this, few studies of this type have included males, yet previous work (Aguilar-Arguello et al. 2019) and this study suggests that males may be more mobile than females, possibly because they actively search for mates at this life stage (Jackson and Pollard 1997), and this is something that should be considered in future work. We observed that males were more active than females and subadults, especially among *Trite* individuals, in which males tended to be more skittish (personal observation).

If salticids are motivated and capable of choosing and completing difficult detours in which visual contact with the goal is lost, we believe they will exhibit 3 key components. These are the initial heading (to some extent, as discussed below), their final choice coinciding with the initial heading, and the fact that they re-orient toward the goal during the detour. However, this combination appears to be cognitively challenging: only 3 *Marpissa* and 12 *Trite*

performed all 3, while 87% ($n = 101$) of 116 spiders tested lacked at least one of these 3 components in their detour.

Although we predicted that spiders would be able to discriminate lures and associate their location with the goal platform while still on the starting platform, the proportion of decided spiders did not differ from that of undecided individuals in either species, nor was this affected by route. This suggests that either: (1) the initial heading is not a good indicator of decision-making regarding chosen route, or (2) that the initial heading indicates a decision, but is often unclear because spiders are not motivated enough to follow the entire route.

In relation to the first hypothesis, that initial heading is a poor indicator of decision-making regarding the chosen route, Tarsitano and Jackson (1994) observed that, while scanning, *Trite* (and *Portia*) first focuses on the goal and then fixates on the different components of the detour, making it difficult to determine a variable that depicts the chosen route during the scanning stage. Thus,

Table 2. Results from comparisons of the probability to choose the short-lured route in *Trite* and *Marpissa* spiders with the other 3 routes, and comparisons between probabilities of choosing routes by length and/or presence of lure

	Log-odds	SEM	*Z*	*P*
*Trite**				
Comparisons between routes				
Long-lured/short-lured	−1.232	0.429	−2.868	0.012
Long-control/short-lured	−2.489	0.736	−3.376	0.002
Short-control/short-lured	−0.182	0.302	−0.602	0.901
Comparisons between route variables				
Control-routes/lured-routes	−0.717	0.428	−1.674	0.210
Short-routes/long-routes	1.767	0.428	4.124	0.0001
Interaction[a]	−0.535	0.428	−1.249	0.429
General dataset (*Marpissa*)**				
Comparisons between routes				
Long-control/long-lured	−0.559	0.361	−1.546	0.297
Short-lured/long-lured	−0.336	0.338	−0.995	0.649
Short-control/long-lured	−0.336	0.338	−0.995	0.649
Comparisons between route variables				
Control routes/lured routes	−0.279	0.257	−1.089	0.618
Short routes/long routes	−0.056	0.257	−0.22	0.995
Interaction[a]	−0.279	0.257	−1.089	0.618
Dataset for completed routes (*Marpissa*)***				
Comparisons between routes				
Long-control/long-lured	−0.559	0.626	−0.893	0.71
Short-lured/long-lured	−5.13e−06	0.534	0	1
Short-control/long-lured	−5.13e−06	0.534	0	1
Comparisons between route variables				
Control routes/lured routes	−9.225	47.510	−0.194	0.860
Short routes/long routes	−8.127	47.510	−0.171	0.878
Interaction[a]	−8.820	47.508	−0.186	0.867

Marpissa: data from all individuals that chose a route (general dataset) and from completed routes dataset. *P* values by route:, *Long-lured ($n = 7$, $P = 0.132$), long-control ($n = 2$, $P = 0.037$), short-lured ($n = 24$, $P = 0.452$), short-control ($n = 20$, $P = 0.377$)., **Long-lured ($n = 21$, $P = 0.333$), long-control ($n = 12$, $P = 0.190$), short-lured ($n = 15$, $P = 0.238$), short-control ($n = 15$, $P = 0.238$)., ***Long-lured ($n = 7$, $P = 0.28$), long-control ($n = 4$, $P = 0.16$), short-lured ($n = 7$, $P = 0.28$), short-control ($n = 7$, $P = 0.28$).
[a] Model accounts for the interaction between route length and lure incidence.

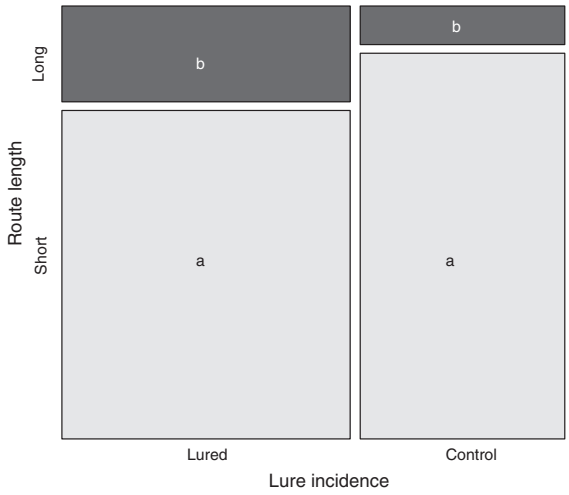

Figure 4. Mosaicplot of the frequency of choices for the 4 different routes in *Trite planiceps*. Horizontal axis depicts the proportion of total *Trite* tested that went toward lured or control routes. Vertical axis depicts the proportion of *Trite* that used long or short routes. The total area of each shaded section depicts the combined proportion of the given variables. Letters denote significant differences.

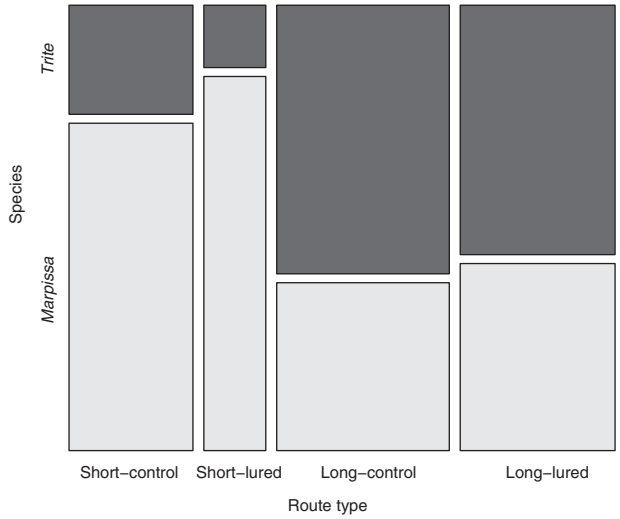

Figure 5. Mosaicplot of proportion of choices for each route in both spider species. Horizontal axis depicts the proportion of total spiders tested that used a given route type. Vertical axis depicts the proportion of each species that used a given route type. The total area of each shaded section depicts the combined proportion of the given variables.

Table 3. Results from the multinomial comparison of the number of individuals of each spider species that chose each route

Comparisons between routes (*Marpissa*/*Trite*)	Log-odds	SEM	*Z*	*P*
Long control/short-lured	−2.261	0.837	−2.720	0.019
Long-lured/short-lured	−1.568	0.546	−2.870	0.012
Short control/short-lured	−0.182	0.474	−0.384	0.969

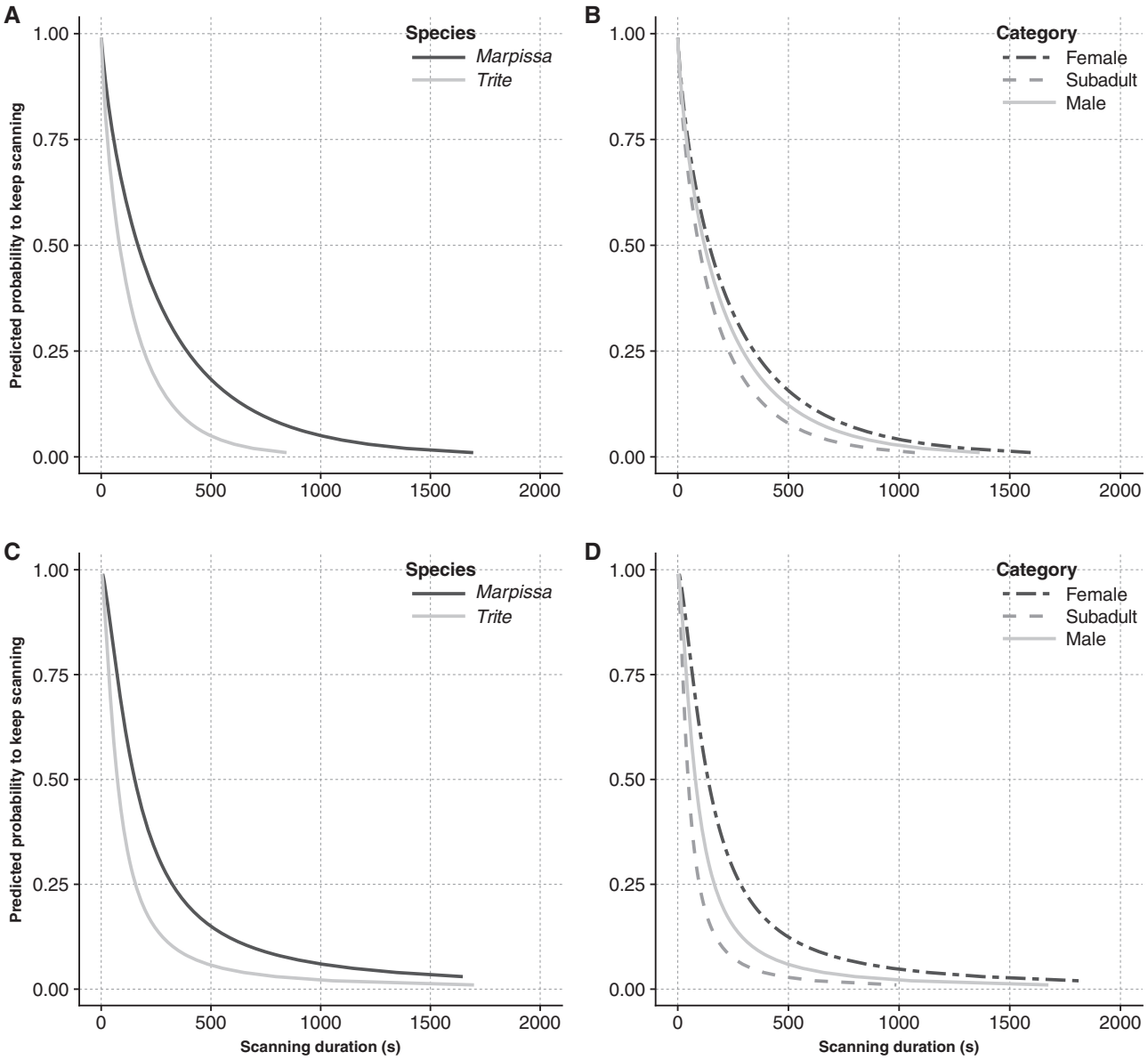

Figure 6. Accelerated failure time model curves depicting the probability of continuing scanning over time for (**A**) all *Marpissa* and *Trite*, irrespective of whether routes were completed, illustrating that *Marpissa* scanned for longer than *Trite* (**B**) combined spider categories of both species, irrespective of whether routes were completed, depicting that the female category scanned the longest (**C**) data from spiders that completed routes for *Marpissa** and *Trite***, (**D**) spider categories from spiders that completed routes***. Values of routes with duration >2000 s not shown: *$n = 2$; **$n = 1$; ***$n = 1$.

decision-making may instead result from the information compiled during the entire scanning process, rather than relying on the last orientation in the scanning routine. If the initial heading is a poor indicator of decision-making, the number of orientations toward a given route may be more indicative of route choice. Our data support the idea that the number of orientations toward a goal during scanning may be a better indicator of choice than initial heading, although how this works is presently unclear. In *Marpissa*, route completion was higher among spiders that performed a high number of orientations, while in *Trite* both the number of orientations and re-orientations were lower for routes that were more frequently chosen.

Evidence for the second hypothesis, that the initial heading is a good decision indicator, is provided by Tarsitano's (2006) work, where *Portia* went to the platform on the same side as their initial heading ("decided") significantly more often than those "undecided" spiders that changed sides from their initial heading (19 versus 7; $\chi^2 = 5.538$, $P = 0.019$; Chi-square test of independence). Our experiment provided limited support for this hypothesis: for both species, but especially among *Trite*, the ratio of decided/undecided spiders did not differ, suggesting that initial heading alone is not always a good predictor of chosen outcome.

Inability to discriminate the presence or absence of prey seems unlikely as an explanation for our observed lack of route preferences. Goal platforms were 17 cm away from the starting platform and salticid vision is accurate within 30 cm (Jackson and Blest 1982). We also doubt that detour length was too challenging, as similar detour lengths have been tested, even with a hidden lure after leaving the starting platform (Tarsitano and Jackson 1997 = 139 cm; Cross and Jackson 2016 = 77.5 cm). However, previous successful

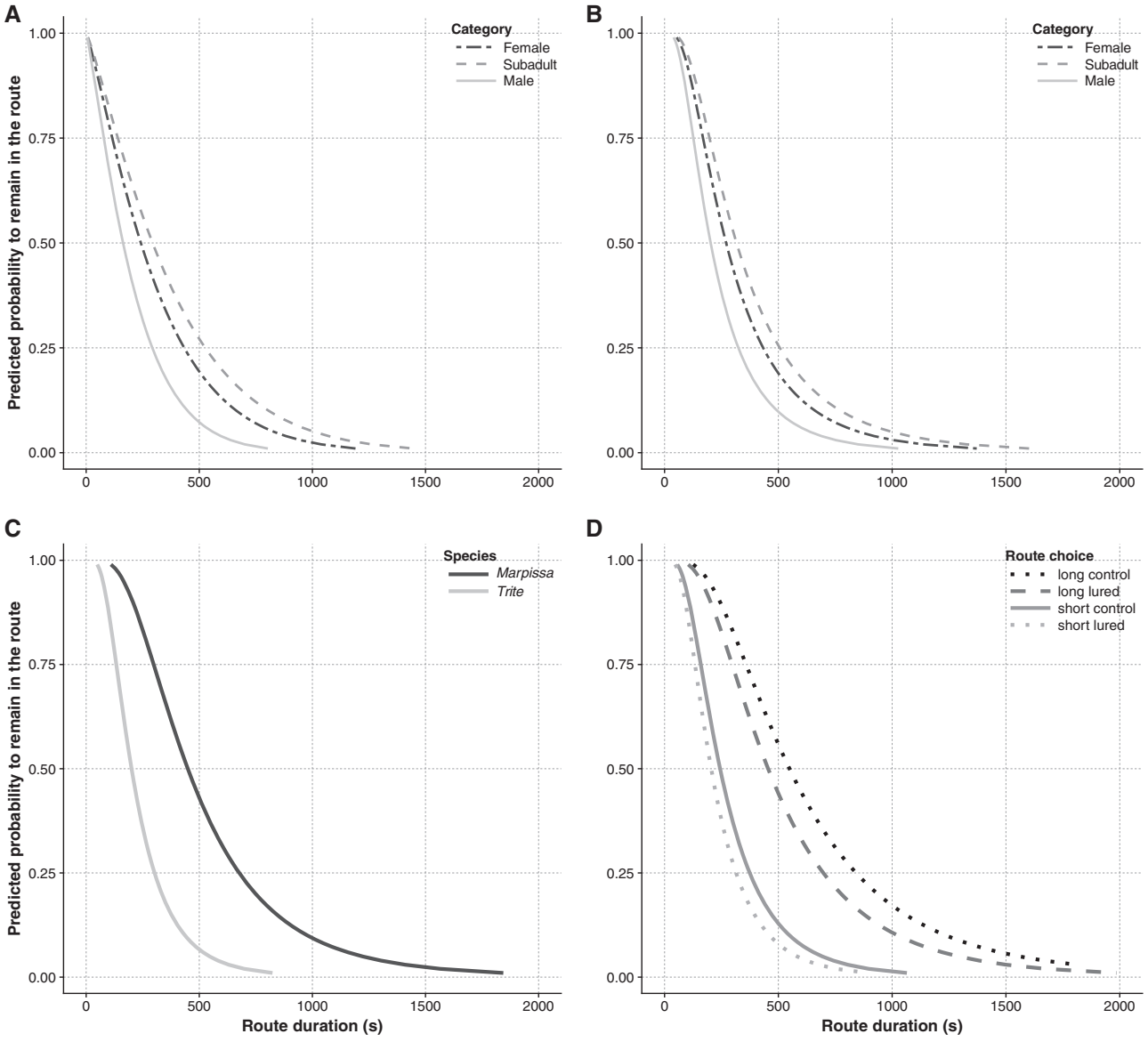

Figure 7. Accelerated failure time model curves depicting the probability of continuing on the chosen route over time for each spider category spiders for (**A**) all spiders, irrespective of whether routes were completed, depicting that route duration was lower in males than females and (**B**) spiders that completed routes only, also depicting that route duration was lower in males than females. (**C**) Species differences between *Marpissa* and *Trite* that completed routes, depicting that *Marpissa* spent longer *en route* than *Trite* and (**D**) route category for spiders that completed routes (data not shown for 2 individuals choosing long-control route, as these lasted >2000 s), depicting that spiders choosing long routes took longer than those choosing short routes.

experiments have been on *Portia* and other Spartaeinae genera, which have exceptional cognitive ability among salticids (Jackson and Pollard 1996; Jackson and Cross 2011), and despite this, the execution of long detours with a hidden lure is difficult for *Portia* (Tarsitano and Jackson 1997). Non-spartaeines, including *Trite* and *Marpissa*, have performed well in detours up to 35 cm (Tarsitano and Jackson 1992), and *Trite* has completed 125 cm-long detours when a moving lure was visible throughout (Tarsitano and Jackson 1994). Possibly what made the present experiment especially difficult was that the lure was visible only from the starting platform, so spiders had to remember the goal's location.

Detouring requires the association of secondary objectives with the primary objective and the use of spatial memory to remember the exact location of the goal (Hill 1979), but visual input may require constantly updating (i.e., re-orientations) to keep motivated and maintain associations. Our data suggest that performing re-orientations is a strong indicator of motivation: *Marpissa* individuals that completed routes (34%) re-oriented to the goal platform more often than those that did not (Supplementary Figure S3). In the case of complex detours, once visual contact with the goal is lost, the association between secondary and primary objectives may be severed, such that the spider cannot keep track of the detour. However, *Portia* and a few Spartaeinae species can follow long and intricate detours without the need to constantly update the primary goal's location (Jackson and Wilcox 1993) and without experience (Tarsitano and Jackson 1997; Cross and Jackson 2016). In contrast, non-spartaeines (including *Trite* and *Marpissa*) can only solve spatial tasks with visual access to a moving prey or when they have had previous experience (Nakamura and Yamashita 2000; Skow and Jakob 2005; Hill 2006; VanderSal and Hebets 2007; Liedtke

and Schneider 2014). Coupling results from those previous studies and ours, we suggest that the species used here can also perform detours as complex as those made by *Portia*, but may require experience to achieve this demanding spatial task. What it is surprising in *Portia* is its ability to plan ahead of time, and its ability to associate visual cues without previous experience. This could be unique not only among salticids, but among invertebrates.

Variation in spatial performance across salticid species is known. For example, despite its ability to complete different types of simple detours (Hill 1979), *Phidippus audax* failed in detours that required initially moving away from the goal for the correct detour (reverse-route detours; Carducci and Jakob 2000), which can be solved by *Trite* (Tarsitano and Jackson 1994). This variation in spatial ability has been attributed to the environmental structure in which each species lives (Tarsitano and Andrew 1999), with complex habitats presenting a more cognitively challenging navigational milieu (Gauin and FitzGerald 1986; Costanzo et al. 2009; Schwarz and Cheng 2010; Clarin et al. 2013; Schultheiss et al. 2016). The relationship between habitat attributes with performance in our study species fits this model, although significantly more comparative work in this area is needed. For instance, *Marpissa*'s struggle to complete the route may be a consequence of the lack of vertical routes in their natural environment, which primarily consists of small rounded rocks and a few pieces of driftwood. All *Trite* completed the routes and performed faster than *Marpissa*, which may be facilitated by adaptations to navigate within the vertical flax leaves that characterize its habitat.

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Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

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Original Article

Risk assessment and the use of novel shortcuts in spatial detouring tasks in jumping spiders

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Selection on individuals that incorporate risk to quickly and accurately make a priori navigational assessments may lead to increased spatial ability. Jumping spiders (Araneae: Salticidae) are characterized by their highly acute vision, which mediates many behaviors, including prey capture and navigation. When moving to a specific goal (prey, nest, a potential mate, etc.), salticids rely on visual cues and spatial memory to orient in 3-dimensional space. Salticid spatial ability has been studied in homing and detour tasks, with *Portia* being considered one of the most skillful genera in terms of spatial ability in the family. Commonly living in complex environments, salticids are likely to encounter a wide variety of routes that could lead to a goal, and, as selection favors individuals that can accurately make assessments, they may be able to assess alternative route distances to select the most efficient route. Here, we tested whether 2 salticid species (*Portia fimbriata* and *Trite planiceps*) can discriminate and assess between different available routes by their length, and riskiness to escape from a stressful scenario. Results suggest that while *Portia* is more likely to choose the easiest and shortest escape routes, *Trite* is faster in both decision making about which route to take, and to escape. However, some individuals were able to use novel shortcuts instead of the routes expected, with *Portia* containing a higher proportion of shortcut-takers than *Trite*. These differences in spatial ability seem to correspond with the environmental complexity inhabited by each species.

Key words: **cognition, decision making, detour behavior, environmental complexity, route choice, salticid.**

INTRODUCTION

Assessment is the process by which animals evaluate perceived stimuli, converting them to an informational state to determine a specific level of risk or benefit (Blumstein and Bouskila 1996), while decision making is a cognitive process that allows animals to evaluate their environment, so they can avoid less favorable situations. Thus, decision making follows assessment and precedes observable behavior (Blumstein and Bouskila 1996). Because of increased ability to take the most efficient route to a goal, selection favors those individuals that can more quickly and accurately make assessments (Helfman 1989; Lima and Bednekoff 1999; Mirza and Chivers 2001; Brown 2003; Golub and Brown 2003). For example, in a food gathering task, selection of inefficient routes results in prolonged foraging, higher energetic cost, decreased time spent on other activities, and increased predation risk (Gibson et al. 2007).

Efficient route use has been observed in bees that integrate information about flight path vectors ("path integration") to navigate to the colony or a food source (Cartwright and Collett 1983), allowing them to make novel shortcuts, even if they cannot see the goal (Dyer 1991; Menzel et al. 2005, 2011). Similarly, shortcuts have been observed in desert ants (Wehner and Wehner 1990) and wandering spiders (Seyfarth et al. 1982). In these cases, proprioceptive mechanisms are used, and the distance assessment of the alternative routes is only done after experience. Here, we investigate whether invertebrates with no previous experience can assess different routes beforehand and follow the most efficient route to reach a goal, without the use of path integration.

Animals that pounce on their prey, such as jumping spiders (Salticidae), are ideal subjects to investigate decision making. Salticids have a highly developed visual system (Land et al. 2012) and perform precision jumps for predation and locomotion, accurately assessing the distance to the landing point (Nabawy et al. 2018). Furthermore, when a salticid identifies a prey, it is sometimes forced to take a detour, as the direct route is either inaccessible (Tarsitano and Jackson 1997), or disadvantageous (Jackson and Wilcox 1993;

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Jackson and Pollard 1996). Salticid detours are preceded by scanning behavior which is characterized by a systematic movement of the body in order to visually inspect its surroundings (Tarsitano and Andrew 1999). Scanning is useful for visual inspection and route selection, but is also a crucial stage for navigation, as the individual potentially plans the route ahead of time (Cross and Jackson 2016). Previous detour-related tasks have shown that salticids can discriminate between routes that lead to a moving or nonmoving prey item from routes that do not (Tarsitano and Jackson 1992, 1994, 1997; Tarsitano and Andrew 1999; Tarsitano 2006), but work to date has not considered risk assessment in detour tasks.

Commonly living in complex environments, salticid ability to find the best route out of a vast number of alternative pathways could be crucial to save energy and time, and avoid predation. Therefore, salticids may be able to assess, beforehand, alternative routes to select the optimum route. While detouring is a spatial ability apparently widespread among the Salticidae, there is a particular genus that stands out due to its exceptional cognitive abilities and its behavioral flexibility (Jackson and Pollard 1996; Jackson and Cross 2011). *Portia* lives in complex rainforest habitats in which it preys upon spiders (Jackson and Wilcox 1990; Harland and Jackson 2000). To reach prey, *Portia* can perform complex detours spanning over a meter, while losing sight of its prey for more than 80 min (Jackson and Hallas 1986a; Jackson and Wilcox 1993). This suggests not only an outstanding sense of orientation in 3-dimensional space, but also spatial memory due to the spider's need to move out of line-of-sight of the prey to follow the detour.

Here, our main objective was to determine if salticids can a priori assess route distance and riskiness, but our study differs from previous work in that there was no clear best goal (e.g., prey) which was reached by a single correct route; rather the goal itself was to choose the most efficient (or least risky) way out of a stressful situation. Our routes were also discontinuous, being made up of dowels, such that the problem may be conceived of as a series of subgoals which needed to be connected in advance in order to achieve the least risky outcome (escape) which was, in itself, identical for all routes. We first tested if salticids differentiate the distance between the dowels and choose a route representing the safest option. Second, we tested whether they can discriminate between different routes according to length, and choose the most suitable one in order to escape a stressful scenario. Additionally, we explored whether there are intraspecific and interspecific differences in route assessment. Being from a complex habitat (Jackson and Blest 1982), and known for its cognitive ability (Jackson and Pollard 1996; Jackson and Cross 2011), we predicted that *Portia fimbriata* would be more effective at making efficient route choices compared with a salticid from a less complex habitat and not known for exceptional cognitive ability, *Trite planiceps*. Our prediction is based on the clever foraging hypothesis, which postulates that individuals living in more complex environments have better neurobiological navigational abilities (Striedter 2005; Park and Bell 2010). As salticid performance improves with knowledge about the environment (Edwards and Jackson 1994; Aguilar-Arguello et.al 2018), we also predicted that adults would outperform subadults. Additionally, we predicted that females would outperform males, as they are typically the more motivated sex, at least in predation-based or learning tasks (Jackson and Wilcox 1990; Jackson and Pollard 1996; Jakob and Long 2016).

METHODS

Test animals and maintenance

Experiments were carried out from 0800 to 1300 h in the laboratory at the University of Canterbury. *Trite planiceps* Simon is a large (6–13 mm) salticid endemic to New Zealand and is typically found in coastal areas where it inhabits the rolled-up flax leaves of *Phormium tenux* and *Cordyline* spp. (Forster 1979). *Trite planiceps* were field collected in Christchurch, and were transferred to the laboratory, where they were housed individually in 1 L transparent plastic containers. Individuals were held in captivity for at least one week before testing. Spiders were fed once a week with 2 adult *Musca domestica*. Water supply was available through a cotton wick submerged in water which protruded into the container.

Portia fimbriata Doleschall is a large (6–11 mm) salticid from the rainforests of Northern Australia (Jackson and Hallas, 1986a). *Portia fimbriata* were lab-reared and, being predominantly araneophagic (spider-eating), were fed a combination of *Musca domestica* and a *Badumna longinqua* spider once a week. Individuals were housed as above.

Test arena

Salticid aversion to water is frequently used as a motivational tool in detour experiments (Cross and Jackson 2016). Here our aim was for spiders to choose a route to escape the stressful scenario of being surrounded by water by getting to the platform edge, rather than choosing a route to a specific target goal, such as prey. Our trials were performed in a 43 × 43 × 7 cm plastic container (pool) filled with water to a depth of 6 cm. From a central starting platform (PVC dowel, 9 cm high × 3.5 cm diameter), 4 possible escape routes extended to each of the 4 sides of the pool. Escape routes consisted of a series of PVC dowels (7 cm high × 1 cm diameter) protruding 1 cm from the water. These led to identical high-resolution pictures of foliage which surrounded the pool to both motivate the spiders to exit the pool and to provide visual obstruction of external visual stimuli. To account for directional biases, we rotated the pool to face North, South, West, or East at every trial. Rotations were randomized in blocks, each containing the 4 directions assigned in random order. To begin each trial, we gently placed a spider on the starting platform with a paintbrush. Spiders always rotated to observe their surroundings for between 50 to 220 s (first and third quartile) before choosing an escape route.

Each trial lasted up to 60 min, except if a spider was still on a route at this time, in which case we continued the trial until the spider reached the edge (maximum time: 110 min). If 60 min elapsed without the spider leaving the starting platform, the trial was aborted and the spider was retested (up to 4 times/day). In the rare cases in which the spider jumped into the water or missed a safe landing, we relocated it with a paintbrush to the dowel from which it had jumped. Relocation was only allowed twice during each trial; otherwise, the individual was tested at a later date.

All trials were recorded with a webcam (Logitech C920 HD Pro) placed over the arena. The variables scored from video were route duration (time from leaving the platform to reaching an edge by using a route), the chosen route, the number of dowels used to reach the edge of the pool (as sometimes the spiders skipped dowels by jumping over the top of one), latency (elapsed time from the start of the trial to the beginning of scanning), and scanning duration (elapsed time from start of visual scanning to jumping off the starting platform). All analyses were done using R version 3.3.3 (R Core Team 2018).

Experiment 1

Our objective was to determine if salticids are able to discriminate a "safe" route from 3 identical but more difficult "risky" routes, and if performance at this task differs depending on species and spider age and sex category (see Supplementary Methods 1.1). Based on typical

salticid jumps being between 1 and 3 cm, the risky routes consisted of 4 dowels separated by 3.5 cm (center to center), while the fourth, safe route, was the same length but contained 8 dowels separated by 1.75 cm, which is close enough for spiders to carefully walk across without jumping (Figure 1A). We tested 47 *Trite* (15 males, 18 females, and 14 subadults) and 62 *Portia* individuals (16 males, 19 females, and 27 subadults) and only analyzed data from completed routes (see Supplementary Methods 1; Supplementary Figures S1 and S2).

To ensure that the position of the dowels was placed at distances that spiders were able to differentiate, we recorded the number of dowels used when the spiders were escaping from the pool. Apart from the probability to choose a specific route, the proportion of dowels used during escape is important because there may be specific differences in jump length. These could alter the perceived difficulty of the routes, under 3 scenarios: 1) If the maximum separation between dowels in the risky routes is too small, we should expect no difference in route choice and also a low proportion of dowels used in both route types. In other words, the risky routes would be as easy as the safe route, the spiders would frequently skip dowels, and routes would be chosen randomly. 2) If the separation distance between dowels in the risky route is too large, we should expect no escapes through risky routes that are too difficult, and the use of the safe route should be the only outcome. Moreover, while using the safe route, spiders would also use a high proportion of dowels. 3) Risky routes are more difficult than safe routes, but still doable. The ideal scenario is providing doable routes, but with different levels of difficulty, so the spiders will be able to identify the safe route from the risky route and then make decisions about which one to take. In this case, the number of safe choices should be higher than random and the proportion of used dowels should be similar and high for both route types.

To investigate if route choice affected whether spiders skipped dowels, we compared the proportion of dowels used with respect to the total number of dowels in the chosen route. For this, we used a generalized linear model (GLM) with a binomial distribution and an additional dispersion parameter (family = quasibinomial) to account for over-dispersion. The proportion of dowels used was the response variable, with species, spider category (male, female, or subadult), the chosen route (safe or risky), and pool direction as the explanatory variables. The model accounted for all second-order interactions, but not for third-order interactions.

To determine if the spiders had a preference to choose the safe route, we used a GLM with a binomial distribution. Here, choice type (1 = safe route, 0 = risky route) was the binary response variable, while species and spider categories were the explanatory variables, accounting for second-order interactions. Given the estimated parameters, we calculated the confidence intervals (CI) of the observed choice type proportions for each species:spider category combination. Whenever the lower limit of the CI was greater than the 0.25 proportion of random choice, we interpreted the spiders of such a group as significantly choosing the safe route more often than by chance at a confidence level of 95%. In the case of specific comparisons of subcategories within each explanatory variable, we used Wald tests or contrasts tests with the "gmodels" package (Warnes et al. 2015); 95% CI were calculated for all estimated parameters.

Survival analyses, using Accelerated Failure Time models (AFT), were applied to scanning duration and route duration variables (Fox 2001). To select the best model, we used the Akaike Information Criterion (AIC; Crawley 2007).

Experiment 2

Our purpose was to determine if salticids can differentiate between different escape routes depending on their length, and if performance at this task differs depending on species and sex/age category. For these tests, methods were as described in Experiment 1, except for the configuration of the pool arena (Figure 1B). Here, spiders had to choose 1 of 4 different routes varying in length and number of dowels, with a straight route (4 dowels; maximum of 5 jumps to reach the pool edge), a zig-zag route (5 dowels; 6 jumps), a diagonal route (6 dowels; 7 jumps), and a curved route (7 dowels; 8 jumps). All dowels within all routes were separated by 3.5 cm. As a consequence, the energetically less expensive and shortest route was the straight route. We tested 42 *Trite* (11 males, 15 females, and 16 subadults), and 58 *Portia* (14 males, 19 females, and 25 subadults). Thirty-one of these 58 *Portia* had been used in Experiment 1, while a similar proportion of *Trite* (23 of 42) were used in Experiment 1.

Recorded variables were as in Experiment 1, with some additions, as spiders did not always use all dowels of the chosen route to escape. Skipping dowels on the chosen route meant less jumps than expected for that route and a shorter or potentially easier route for the spiders, contrary to the objective of the experiment, as a spider

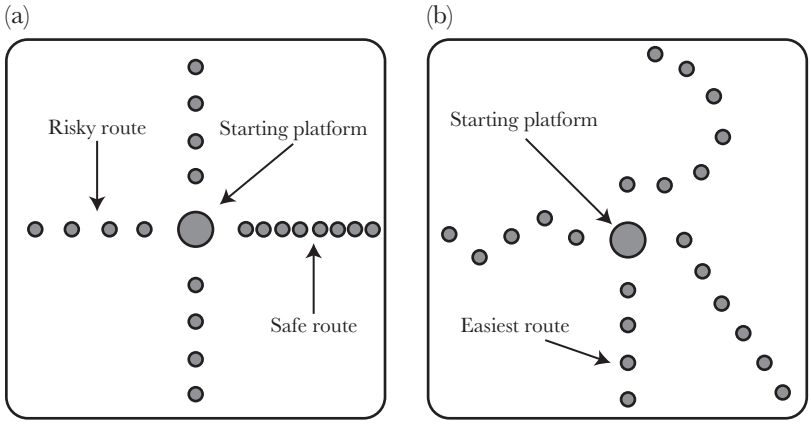

Figure 1
Test arenas for (A) Experiment 1; 1 safe versus 3 identical risky escape routes (dowel separation denotes risk level), and (B) Experiment 2; easy versus increasingly long routes. See Methods for further details.

skipping dowels (i.e., taking a shortcut) could potentially find a relatively easy way to escape even if it chose the longer route. To account for this behavior, we calculated the number of dowels used by the spider divided by the number of dowels within the chosen route, with 1 meaning that the spider used all the available dowels in the escape route. We then included a binomial variable named "shortcut-taking" to separate spiders that took shortcuts (≦ 0.75; labeled as 1), from spiders that did not (>0.75, labeled as 0). The threshold was set at 0.75 because taking shortcuts in the 6- and 7-dowel routes was almost unavoidable, as the last dowels were only 1 cm from the pool's edge and the spiders seldom used these dowels to reach the edge.

Shortcut-taking by the spiders to escape the arena was unexpected and exposed a potential flaw in our experimental design, as route preferences could be biased by spiders that took shortcuts. As a consequence, we performed 2 analyses; the first considering all data, and the second considering only data from nonshortcut-taking spiders. Analyzing both datasets separately not only assessed the behavior of all spiders and nonshortcut-taking spiders, but also allowed us to compare both datasets and make inferences about the effect of the explanatory variables among spiders that took shortcuts.

To test if there was a preference for a specific route depending on different response variables, we used 2 ordinal logistic regressions: for all data and for nonshortcut-taking spiders only. The chosen route was then parameterized as a 4-level ordered categorical response term (according to increasing number of dowels) in a cumulative link (or proportional odds) model (CLM, package: ordinal, Christensen 2018), with the terms spider category, species, and bout duration. Second-order interactions among the explanatory variables were not accounted for, as the AIC value was higher than the selected model. Wald and Likelihood test values were calculated for both CLM models. To make inferences about route preferences for *Portia* and *Trite*, we estimated the cumulative probabilities (*P*) to choose the different routes ordered by length at the intercept (when route duration is equal 0), and their CI at 95% (see Supplementary Methods 2). Thus, a preference to choose the 4-dowel route would be shown if *P* for 4-dowel route was >0.25. A preference for the 5- and 4-dowel route over the 6- and 7-dowel routes would exist if $P > 0.5$, and a preference for using the 6-dowel route or shorter over the 7-dowel route would be shown when $P > 0.75$.

Selection of the CLM including all data was the one with the lowest AIC value when checked for model diagnostics (see Christensen 2015). For comparative purposes, we used the same structure to analyze data from nonshortcut-taking spiders, so model selection was not used in this case. This model had the chosen route as the response variable, with spider category, species, and bout duration as explanatory variables, without interactions.

For both datasets, we analyzed scanning duration and route duration using AFT survival models and we selected the distribution type based on the lowest AIC. For the response variable scanning duration, species, chosen route, and shortcut-taking were the explanatory variables. Second-order interactions among the explanatory variables were not accounted for, as the AIC value was higher than the selected model. For the response variable route duration, species and chosen route were the explanatory variables.

To compare the number of shortcut-taking spiders versus nonshortcut-taking spiders, we used Chi-square tests of independence. The CLM was discarded as an option to analyze route choice, as the "ordinal" nature of this variable is lost and the route choice is biased. In other words, taking shortcuts allowed spiders to take any route and make it novel, invalidating route length and violating the assumptions of ordinal logistic regression (Christensen 2015). Therefore, inferences about route preference were obtained from comparisons of CLM's belonging to general data and nonshortcut-taking spiders only. To compare the scanning duration and route duration among shortcut-taking spiders, we used nonparametric Kruskal–Wallis tests.

RESULTS

Experiment 1

Here, we tested if spiders were capable of discriminating a "safe" route from 3 "risky" routes, and if performance at this task differs depending on species and spider age and sex category. Overall, we found both species and age/sex differences on the routes taken, the probability to stay on a given route, and on the time spent scanning a route before embarking on it.

In our GLM analysis of whether route choice affected if spiders skipped dowels, we found that the proportions of dowels used did not differ between spider categories, either for the chosen route or cardinal direction (Supplementary Table S1). The proportion of dowels used in risky (min, max, median; 25–75% quartiles; 0.25, 1.0, 1.0; 0.75–1.0) and safe routes (0.125, 1.0, 0.813; 0.5–1.0) was high, but did not differ between safe and risky routes ($P = 0.764$; Supplementary Table S1). Additionally, *Trite* (0.5, 1.0, 1.0; 0.75–1.0) used a marginally nonsignificantly higher proportion of available dowels ($P = 0.08$; Supplementary Table S1) than *Portia* (0.125, 1.0, 0.75; 0.47–1.0). Overall, we found no significant interactions between explanatory variables (see Supplementary Table S1 for estimated effect sizes).

In *Portia*, the probability to choose risky routes was about 50% (Supplementary Figure S3), while *Trite* showed no preference for the safe route (Supplementary Figure S4). As a result, we were confident that the spatial task of Experiment 1 was challenging, but achievable, for both for salticid agility and cognitive ability. *Portia* females (estimate; CIs reported for all) (0.47; 0.26–0.69) chose the safe route more often than expected by chance, whereas subadults (0.41; 0.24–0.59) and males (0.31; 0.13–0.56) chose the safe route with similar frequencies as the rest of the routes (Supplementary Figure S3). *Trite* females (0.22; 0.07–0.44) and subadults (0.21; 0.06–0.47) exhibited random route choice, while males (0; no data-1) never selected the safe route (Supplementary Figure S4).

Our survival analyses examined time to event data to estimate the effects of covariates on acceleration/deceleration of the survival time (in this particular case, the time in which the spiders end a determined behavioral stage, influenced by an explanatory variable). Explanatory variables were: chosen route, species, and spider category. All second-order interactions were also accounted for in this model. Because salticid scanning is thought to be crucial for navigational planning (Cross and Jackson 2016), we analyzed the time spent scanning. *Portia* was equally likely to keep scanning over time, regardless of route chosen, although as time went on, the probability to remain scanning dropped (Figure 2). The latter effect was similar for *Trite*, but *Trite*'s probability to remain in scanning mode was higher when spiders opted to take the safe route compared with the risky routes (Figure 2). In other words, the probability to keep scanning during trials was significantly affected by the interaction of route choice and species, but not by route choice:category or category:species interactions (Table 1).

In terms of route duration, the AFT model was fitted to a lognormal distribution and chosen route:spider category, and

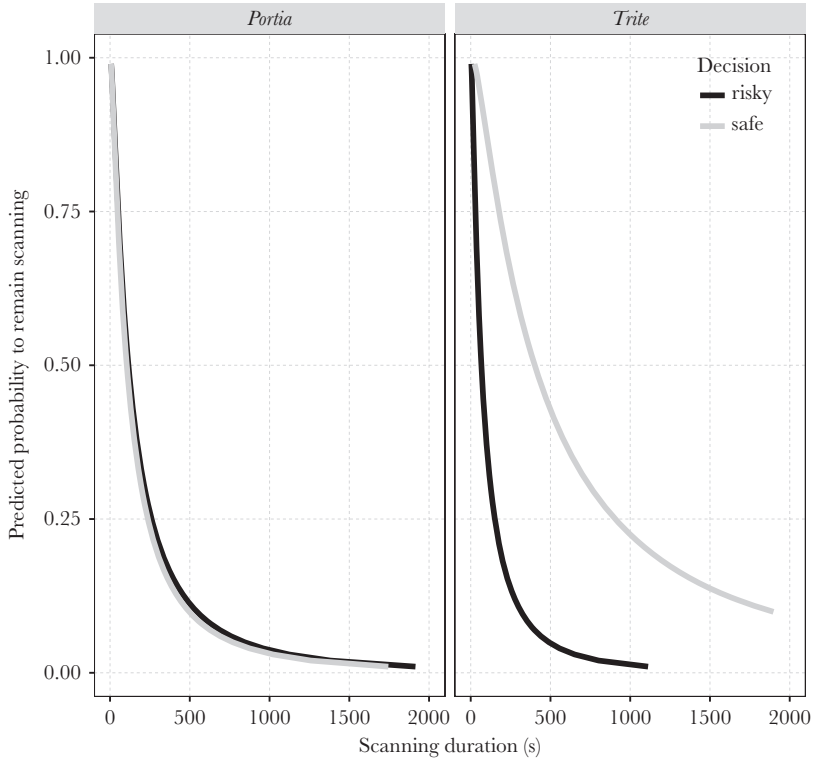

Figure 2
AFT model curves depicting the probability of continuing scanning behavior over time, as a factor of route chosen (risky or safe) in Experiment 1 for *Portia* and *Trite* spiders. *Portia*'s scanning behavior was not affected by route chosen, while *Trite*'s probability to remain in scanning mode was higher when spiders opted to take the safe route compared with the risky routes.

Table 1
Summary table of AFT model with lognormal distribution: scanning duration as a function of route choice, spider category and species for Experiment 1, safe versus risky escape routes. Third-order interactions were excluded. CI = confidence interval at 95%

Variable	Estimate	CI	Z	*P*
Intercept	5.096	4.392–5.800	14.20	<2e−16
Route choice	−0.259	−1.223–0.705	−0.53	0.598
Species (*Trite*)	−0.877	−1.765–0.010	−1.94	0.052
Category (Subadult)	−0.244	−1.112–0.624	−0.55	0.581
Category (Male)	−0.819	−1.814–0.175	−1.61	0.106
Route choice: *Trite*	1.999	0.771–3.227	3.19	0.001
Route choice: Subadult	0.052	−1.102–1.206	0.09	0.929
Route choice: Male	0.325	−1.259–1.911	0.40	0.687
Subadult: *Trite*	0.274	−0.844–1.392	0.48	0.631
Male: *Trite*	0.757	−0.525–2.040	1.16	0.247
Log(scale)	0.174	Not applicable	2.57	0.010

species:spider category were the only interactions included. Spider category and species had a significant effect on the probability to remain on a chosen route. Specifically, *Portia* was more likely to stay *en route* than *Trite* (Supplementary Figure S5A), and females and subadults were more likely to stay on the chosen route than males (Supplementary Figure S5B). We found no significant interactions affecting route duration (Table 2).

Experiment 2

Here, we tested if spiders were capable of discriminating between different escape routes depending on their length, and if performance differed depending on species and spider age/sex category. Overall, we found species differences on the routes taken, with *Portia* opting for shorter routes. There was no difference between species on the time spent scanning a route before embarking on it, but *Portia* was significantly more likely to create novel shortcuts by skipping dowels, and was significantly more likely to stay on its initially chosen route.

When all data (shortcut-taking and nonshortcut-taking spiders) were included (Table 3), the selected CLM was built with the "cloglog" link function. The probability of choosing a given route differed between species, with the odds of *Portia* choosing the 4-dowel route being 1.64 times that of *Trite*, which comparatively chose the longer routes. Spider category had no effect on the probability of choosing any given route, but route duration was related to the

Table 2

Summary table of AFT model with lognormal distribution: route duration as a function of route choice, spider category and species for Experiment 1, safe versus risky escape routes. Third-order interactions and choice type: species interactions were excluded. CI = confidence interval at 95%

Variable	Estimate	CI	Z	*P*
Intercept	5.553	5.051–6.055	21.67	<2e−16
Route choice	−0.508	−1.137–0.121	−1.58	0.113
Species (*Trite*)	−1.042	−1.642–−0.441	−3.40	0.0006
Category (Subadult)	−0.458	−1.110–0.193	−1.38	0.168
Category (Male)	−0.912	−1.643–−0.180	−2.44	0.014
Route choice: Subadult	0.181	−0.682–1.044	0.41	0.680
Route choice: Male	−0.547	−1.687–0.592	−0.94	0.346
Subadult: *Trite*	0.518	−0.325–1.361	1.20	0.228
Male: *Trite*	0.557	−0.365–1.479	1.18	0.236
Log(scale)	−0.106	Not applicable	−1.57	0.116
Specific comparison				
Subadult vs. Male	0.557	0.048–1.066	2.15	0.031

Table 3

Results of ordinal logistic regression model ("cloglog" link) for routes varying in difficulty for all spiders (spiders that skipped dowels, or took shortcuts, and nonshortcut-taking spiders) in Experiment 2. CI = confidence interval at 95% (estimates and CI of estimates from Wald tests). NA = Not applicable.

		CI of estimate						CI of odds ratio	
Variable	Estimates	2.5%	97.5%	Z	*P* (Wald test)	*P* (likelihood ratio test)	Odds ratio	2.5%	97.5%
Species	0.495	0.001	0.988	1.967	0.049	0.046	1.64	1.0	2.7
Category: subadult/female	−0.027	−0.573	0.518	−0.099	0.920	0.538*	NA	NA	
Category: male/female	−0.320	−0.927	0.286	−1.036	0.300				
Route duration	0.0007	0.0001	0.001	2.387	0.017	0.006	1.0007	1.0001	1.001

*The CLM likelihood ratio test estimates the effect of the spider category over the probability to choose each route chosen rather than compare pairs of subgroups (subadult vs. female, male vs. female) shown in the Wald test.

chosen route. In terms of odds ratios, a change of one unit (≡ 1 s) in route duration implies 0.07% increase in odds (0.7% for 10 s or 70% increase in odds for 1000 s) to choose the 5-, 6-, and 7-dowel routes instead of the 4-dowel route. This suggests that, when a spider took a long time to escape, it may have been simply because it chose a longer route instead of the 4-dowel route. In addition, *Portia* chose the 4-dowel route with a likelihood higher ($P = 0.348$) than the 0.25 expected by chance (CIs = 0.279, 0.425). The cumulative probability to choose either 4-, 5-, or 6-dowel routes was also lower than expected by chance in *Portia* ($P = 0.688$; CIs = 0.620, 0.749), meaning that the 7-dowel route was used more frequently than by chance. In the case of *Trite*, the cumulative probability to choose either the 4-, 5-, or 6-dowel route was lower than the 0.75 expected by chance (Figure 3), which indicates that *Trite* preferred the 7-dowel route over the rest of the routes (see Supplementary Table S2).

Furthermore, with the combined shortcut-taking and nonshortcut-taking data, we found no effect of spider species, chosen route, nor their interaction, on the probability to remain in scanning mode (Table 4). However, species had a significant effect on the probability to remain on a chosen route (Table 5), with *Portia* being more likely to remain *en route* than *Trite* (Figure 4A). Route length also significantly affected the probability of the spiders to remain on their chosen escape route, with the shorter (4- and 5-dowel) routes not differing, and having a significantly lower probability for spiders to remain (in other words, a higher probability to escape sooner) than when choosing the longer, 6- and 7-dowel, routes (Table 5, Figure 4B).

When comparing shortcut-takers (39 *Portia* and 18 *Trite*) against nonshortcut-takers, (19 *Portia* and 24 *Trite*) we found that *Portia* was significantly more likely to skip dowels than *Trite* ($X^2 = 5.91$, $P = 0.015$; 67% vs. 43%, respectively), however, no sex/age category within *Portia* was more likely to take shortcuts ($X^2_2 = 0.262$, $P = 0.877$; males: 71%, females: 63%, subadults: 68%). Within *Trite*, males (73%) were significantly more likely to take shortcuts than females (20%) or subadults (44%), although these are based on small sample sizes ($X^2_2 = 7.21$, $P = 0.027$) (see Supplementary Figure S6 for sample sizes and trends).

We then partitioned the dataset to further explore trends within the shortcut-taking and nonshortcut-taking groups. The CLM for nonshortcut-taking spider dataset integrated the "cloglog" link function, showing no significant effect of species, spider category, or route duration on the probability to choose a specific route (Table 6). Nevertheless, *Portia* chose the 4-dowel route with a probability higher than the 0.25 expected by chance ($P = 0.484$; CIs = 0.364, 0.606; Figure 5), while *Trite* exhibited random route choices (see Supplementary Table S2). Similar to our results using the combined data (shortcut and nonshortcut-takers), we found that the probability of nonshortcut-taking spiders to remain scanning the chosen route was not affected by species, route chosen, nor their interaction (Table 4), that nonshortcut-taking *Portia* were more likely to remain on the chosen route than *Trite* (Supplementary Figure S7A), and that route length affected the probability of the spider remaining on that route (Supplementary Figure S7B; Table 5).

Within the subset of spiders that took shortcuts, we found no effect of sex/age category on scanning duration (H_2 = 3.367, P = 0.186) or route duration (H_2 = 1.889, P = 0.389) in *Portia* (Supplementary Figure S8A). Within *Trite*, however, while we found no effect of sex/age category on scanning duration (H_2 = 2.904, P = 0.234), we did find differences in route duration (H_2 = 6.934, P = 0.031; Supplementary Figure S8B), which were driven by female variability in a very small sample (n = 3 female shortcut-taking *Trite*) based on a single slow female, so this should be taken with caution.

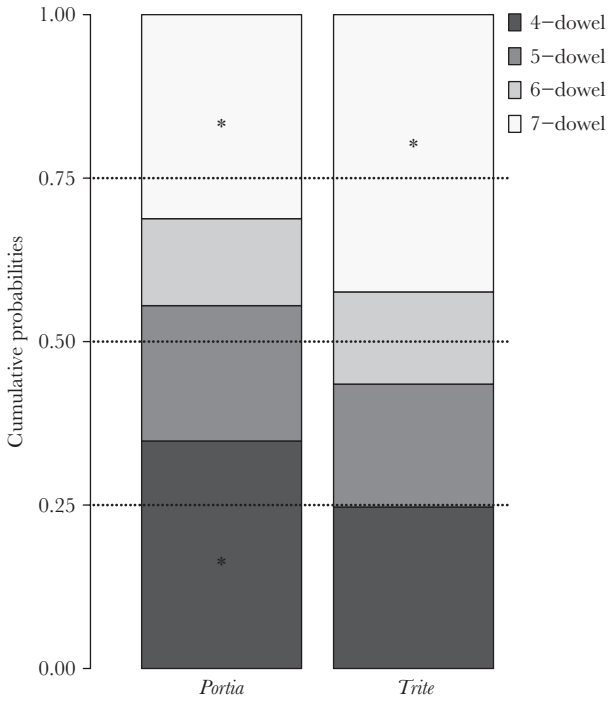

Figure 3
Cumulative probabilities for choosing routes by length calculated from the CLM considering all data set. Dotted lines depict the proportion of safe choices if spiders performed randomly (0.25 for 4-dowel, 0.5 for choosing either 4- or 5-dowel route, and 0.75 for choosing either 4-, 5-, or 6-dowel routes). *denotes the use of each route with a frequency higher than by chance.

DISCUSSION

We demonstrate that salticids are able to assess distance in a spatial context by discriminating the difficulty of discontinuous routes. Furthermore, salticids can devise novel shortcuts or short route options to escape the testing arena. By preferring the safe escape route for Experiment 1, tending to take shortcuts more and preferring the shortest route when it did not take shortcuts in Experiment 2, it seems that *Portia* was either more inclined to make larger jumps or better at assessing spatial tasks than *Trite*.

The physical difficulty of our tests in terms of distance between dowels is unlikely to have been overly challenging for either species. All individuals were able to jump from 1 dowel to another and all were able to escape from the pool, even using the most difficult routes (i.e., risky and 7-dowel routes). Both species have the ability to jump several times the distances used here (*Trite*: up to 150 mm (Taylor and Jackson 1999); *Portia*: up to 80 mm (Jackson and Hallas 1986b). Interspecific differences are thus likely to be either due to differences in rearing conditions (*Trite* were field collected, while *Portia* were lab-reared), spatial or cognitive ability, motivation, or a combination of both of the latter, rather than inability to escape through a difficult route.

Previous detour-related tasks on salticids, including the species tested here, show that they discriminate between routes leading to a prey item from those that do not (Tarsitano and Jackson 1992, 1994, 1997; Tarsitano and Andrew 1999; Tarsitano 2006). Unlike

Table 4
AFT models fitted with loglogistic distribution for Experiment 2. The models include scanning duration as the response variable, whereas routes varying in length and spider species are considered as explanatory variables. The table shows AFT models results including all data (spiders that took shortcuts, and nonshortcut-taking spiders) and, below, for nonshortcut-taking spiders only. CI = confidence interval at 95%. NA = Not applicable.

All data included

Variable	Estimate	CI	Z	P
Intercept	5.199	4.684–5.714	19.79	<2e−16
Route (5-dowel)	−0.527	−1.294–0.239	−1.35	0.18
Route (6-dowel)	−0.287	−1.060–0.484	−0.73	0.47
Route (7-dowel)	−0.398	−1.236–0.440	−0.93	0.35
Species (*Trite*)	−0.504	−1.377–0.367	−1.13	0.26
5-dowel: *Trite*	0.406	−0.850–1.662	0.63	0.53
6-dowel: *Trite*	−0.343	−1.668–0.981	−0.51	0.61
7-dowel: *Trite*	−0.075	−1.312–1.162	−0.12	0.91
Log(scale)	−0.434	NA	−5.18	2.2e−07
Data from nonshortcut-taking spiders only				
Intercept	5.492	4.713–6.271	13.82	<2e−16
Route (5-dowel)	−0.075	−1.341–1.189	−0.12	0.906
Route (6-dowel)	−0.561	−2.137–1.014	−0.70	0.485
Route (7-dowel)	−0.546	−1.911–0.819	−0.78	0.433
Species (*Trite*)	−0.473	−1.620–0.674	−0.81	0.419
5-dowel: *Trite*	−0.205	−2.028–1.616	−0.22	0.825
6-dowel: *Trite*	−0.382	−2.687–1.921	−0.33	0.745
7-dowel: *Trite*	NA	NA	NA	NA
Log(scale)	−0.302	NA	−2.34	0.019

Table 5

AFT models fitted with lognormal distribution for Experiment 2. The models include route duration as the response variable, whereas routes varying in length and spider species are considered as explanatory variables. The table shows AFT models results including all data (spiders that took shortcuts, and nonshortcut-taking spiders) and, below, for nonshortcut-taking spiders only. CI = confidence interval at 95%

All data included

Comparisons	Estimate	CI	Z	*P*
Portia/*Trite*	−0.633	−1.031–−0.235	−3.12	0.001
4-dowel/5-dowel	−0.005	−0.531–0.519	−0.02	0.982
4-dowel/6-dowel	0.572	0.001–1.143	1.96	0.049
4-dowel/7-dowel	0.779	0.261–1.296	2.95	0.003
5-dowel/6-dowel	0.578	−0.009–1.166	1.93	0.054
5-dowel/7-dowel	0.784	0.247–1.322	2.86	0.004
6-dowel/7-dowel	0.206	−0.381–0.794	0.69	0.490
Data from nonshortcut-taking spiders only				
Portia/*Trite*	−0.779	−1.333–−0.224	−2.75	0.005
4-dowel/5-dowel	0.192	−0.425–0.809	0.61	0.541
4-dowel/6-dowel	0.898	0.108–1.688	2.23	0.025
4-dowel/7-dowel	0.217	−0.670–1.103	0.48	0.632
5-dowel/6-dowel	0.706	−0.148–1.560	1.62	0.103
5-dowel/7-dowel	0.024	−0.902–0.950	0.05	0.959
6-dowel/7-dowel	−0.682	−1.767–0.403	−1.23	0.218

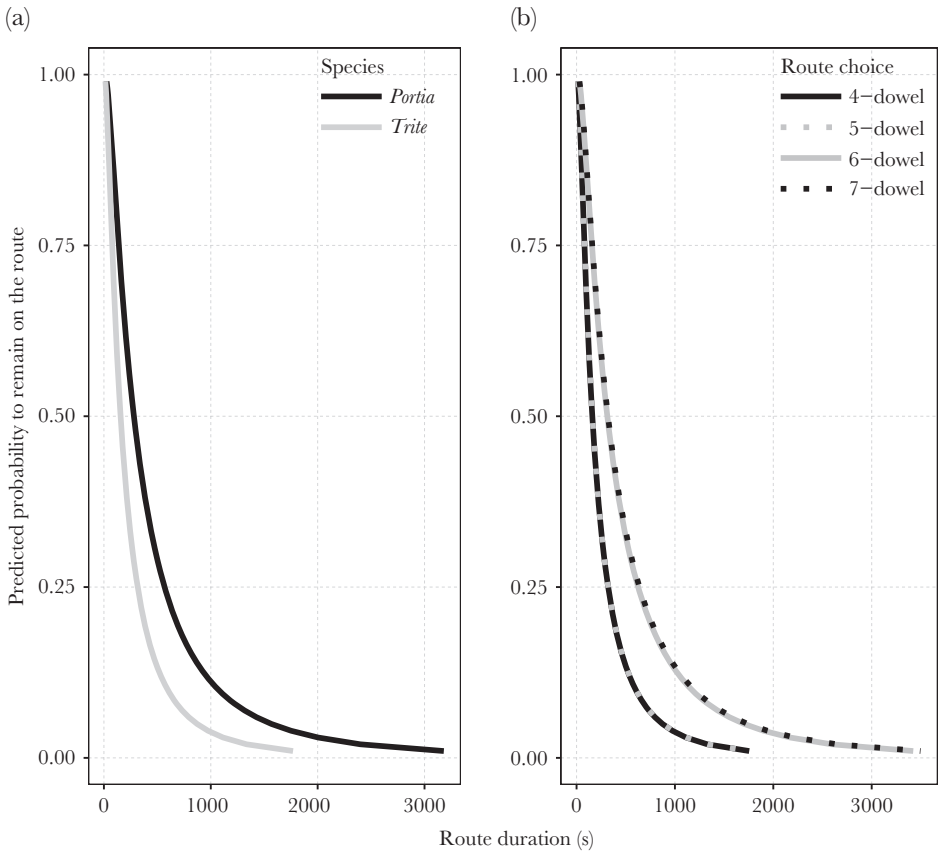

Figure 4

AFT model curves for Experiment 2, depicting the probability of continuing on the route chosen over time for (A) all *Portia* and *Trite* spiders and (B) routes varying in length for both species combined (including data from spiders that skipped dowels, or took shortcuts, and those that did not). *Portia* was more likely to remain on a chosen route than *Trite*, and time on route for shorter routes were similar to each other and shorter than for the longer routes.

in those studies, we did not restrict our testing solely to adult females and there was no clear best goal at the end of a single correct route. Instead, the goal was to choose the most efficient, or least risky, escape from a stressful situation. Additionally, the routes were discontinuous, leading to the problem being conceptualized as a series of subgoals or route attributes that had to be connected in advance to achieve the least risky outcome (escape) which was, in itself, identical for all routes. The location of a subgoal (or secondary

Table 6

Results of ordinal logistic regression model ("cloglog" link) for spiders that took shortcuts in Experiment 2, for routes varying in length. CI = confidence interval at 95% (estimates and CI of estimates from Wald test). NA = Not applicable.

		CI of estimate						CI of odds ratio	
Variable	Estimates	2.5%	97.5%	Z	*P* (Wald test)	*P* (likelihood ratio test)	Odds ratio	2.5%	97.5%
Species	0.507	−0.271	1.28	1.276	0.202	0.203	1.66	0.8	3.6
Category: subadult/female	−0.242	−1.009	0.524	−0.620	0.536	0.440	NA	NA	
Category: male/female	−0.724	−1.815	0.366	−1.302	0.193				
Route duration	0.0001	−0.0005	0.0008	0.369	0.712	0.705	1.0001	0.8	3.6

*The CLM likelihood ratio test estimates the effect of the spider category over the probability to choose each route chosen rather than compare pairs of subgroups (subadult vs. female, male vs. female) shown in the Wald test.

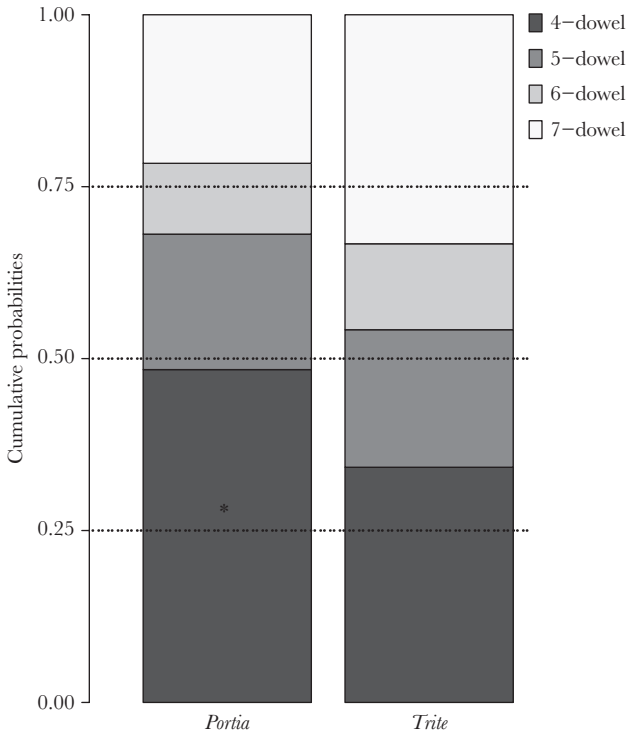

Figure 5

Cumulative probabilities for choosing routes by length calculated from the CLM considering nonshortcut-taking spiders. Dotted lines depict the proportion of safe choices if spiders performed randomly (0.25 for 4-dowel, 0.5 for choosing either 4- or 5-dowel route, and 0.75 for choosing either 4-, 5-, or 6-dowel routes). *denotes the use of each route with a frequency higher than by chance.

objective) must therefore be stored in memory (Hill 1979), and, as the number of subgoals increases, more memory capacity is required. Thus, our tests should require more complex cognitive processing than continuous routes that lead or do not lead to a single salient outcome. Perhaps it is because of these differences that we found less clear-cut effects than previous studies (e.g., Tarsitano and Jackson 1992, 1994, 1997; Tarsitano and Andrew 1999; Tarsitano 2006).

While rearing salticids in a social environment (Leidtke and Schneider 2017) and with environmental enrichment (Carducci and Jakob 2000) makes them perform better in learning tasks, rearing condition does not seem to adequately explain our results. All spiders were housed with environmental enrichment, lab-reared spiders were reared socially for the first few instars of their life (*Portia* eat each other so this is not feasible for their entire life-span), and all tested spiders were naïve to the apparatus. Our experience in rearing salticids has typically been that after several generations within the lab, salticids perform more poorly. Our *Portia* were third-generation lab-reared, yet outperformed wild-caught *Trite*. Another possibility to explain our results is that salticids were able to count the number of dowels forming an escape route, and make decisions based on this. It is known that a related species to *Portia fimbriata*, *P. africana*, can classify up to 3 prey as discrete number categories (Nelson and Jackson 2012, Cross and Jackson 2017). It remains unclear whether failure of higher numerical ability is a cognitive or motivational limitation. While the possibility that our spiders were able to count dowels is tantalizing, it is impossible to determine whether route preference was driven by the number of dowels within the route. Nonverbal ability to discretely count objects ("subitize") tends to break down above 4 (Gallistel and Gelman 2000; Dacke and Srinivasan 2008), which was the minimum number of dowels used in these tests. Thus, it is unlikely that our *P. fimbriata* could numerically distinguish between routes. Instead, these may have been assessed in terms of the "quantity" of the continuous variables created by having more dowels (i.e., surface area, volume, areas of contrast, etc.). Our results indicate that *Portia* is likely able to assess a route by its length, and by the distance between dowels, and may be better able at evaluating a path containing multiple subgoals (dowels) than *Trite*, which, in turn, may tend to assess only from 1 dowel to the next without searching for alternative subgoals, resulting in less incidence of taking shortcuts.

Portia was generally slower at escaping the pool arena, possibly because it adopts an unusually slow, choppy, gait when walking (Jackson and Blest 1982, Jackson and Hallas 1986b). Nevertheless, several strands of evidence suggest that our experiments posed problems more easily solved by *Portia* than *Trite*: in Experiment 1, *Portia* took safe routes above chance levels, yet scanning duration for this species was similar for both safe and risky routes. In contrast, *Trite*'s route choice was random, but when it did choose the safe route, prior to exiting the starting platform it scanned the route longer compared with risky routes and compared with *Portia*. In salticids, the duration of visual scanning is correlated with decision making and planning ahead of time (Tarsitano and Andrew 1999; Cross and Jackson 2016). This suggests either that *Portia* was more flexible and willing to take risks "on the fly," or was faster at assessing its visual surroundings to make an "informed" risk-averse decision compared with *Trite*. Furthermore, in Experiment 2, when using the entire dataset, *Portia* was more likely than *Trite* to escape via shorter routes. Additionally, for spiders that took shortcuts, decision making in both species did not differ for the 5-, 6-, and 7-dowel routes, yet *Portia* preferred the 4-dowel route, while *Trite* showed no

preference. Results of Experiment 1, in which *Portia* used a significantly lower proportion of dowels compared with *Trite*, corroborate findings of Experiment 2, in which *Portia* was significantly more likely to take shortcuts than *Trite*. This may suggest that *Portia* has better facility to "mentally" create shortcuts or assess easier routes than *Trite* (i.e., route planning, Cross and Jackson 2016). Our results are in line with a previous comparative detour task in which *Portia* exhibited better visual discrimination for nonmoving prey than *Trite* (Tarsitano and Jackson 1994). Interestingly, when comparing results from data containing both spiders that took and did not take shortcuts with those that did not take shortcuts only, we found that spiders of both species that took shortcuts exhibited a preference for the 7-dowel route. As the longest route, we expected the 7-dowel route to be the less preferred option. It is possible that the shape of the route may have provided a wider range of alternative routes for spiders due to the curved arrangement of the dowels. This meant that, in practice, skipping dowels on the longest route required a shorter jump than skipping dowels on the other routes. Coupled with this, the angle as the route neared the pool edge meant that the distance to the edge from the fifth and sixth dowels was short, making it relatively easy to jump to the edge from these 2 dowels, thus skipping the seventh dowel.

Due to psychophysical and behavioral evidence that females are better performers than males (Jackson and Hallas 1986b; Jackson and Pollard 1996; Zurek et al. 2010; Zurek and Nelson 2012; Jakob and Long 2016), we expected females to outperform males and subadults, and also that adults would outperform subadults, because experience seems to improve behavioral outcomes in salticids (Edwards and Jackson 1994; Skow and Jakob 2005; Hill 2006). Possibly because we used neither potential prey nor conspecifics (often used as motivators in salticid studies) in our tests, sex and age differences were not apparent in our cognitively demanding experimental set-up, other than males tended to complete routes faster—possibly because adult males may be more active due to their role in actively searching for mates at this life stage (Jackson and Pollard 1997). The other exception, that shortcut-taking females were marginally slower to escape than males and subadults, should be taken with caution, as this was based on a single female (from 3) that took a very long time.

Differences in spatial ability selected by characteristics of the environment have been observed in several taxa (Gauin and FitzGerald 1986; Costanzo et al. 2009; Schwarz and Cheng 2010; Clarin et al. 2013). For example, despite the fact that *Melophorus* sp. and *M. bagoti* are closely related species of desert ants, they rely on different navigation mechanisms: *M. bagoti* inhabits visually rich environments and depend mainly on visual landmarks for orientation, whereas *Melophorus* sp. lives in visually barren environments (Schwarz and Cheng 2010; Schultheiss et al. 2016) and primarily relies on path integration. Tarsitano and Andrew (1999) proposed that *Portia*'s spatial prowess may be selected for as a consequence of having to search for mates or prey in a complex environment containing large trees (Jackson and Blest 1982), as suggested by the clever foraging hypothesis (Striedter 2005; Park and Bell 2010). In the rainforest of Australia, *Portia* has numerous predators and considerable competition for prey (Jackson and Blest 1982). In contrast, in the temperate areas of New Zealand, where *Trite* is found, there is significantly lower competition for food, and predation is most likely limited to birds and a few invertebrates, including dragonflies and earwigs, 2 parasitoid wasps, and 3 species of spider (Taylor 1997; Taylor and Jackson 1999). It is tempting, but premature, to conclude that the simpler environment inhabited by *Trite*, consisting of flax bushes to a height of about 2.5 m (Taylor and Jackson 1999), could lead to different spatial ability than *Portia*. To adequately answer this question, we must assess whether salticids can plan entire routes before leaving a starting platform, rather than making adjustments *en route*. Our findings about willingness to take shortcuts suggest that further refinements are needed to address whether interspecific differences in shortcut-taking are either due to premeditated decisions, or to interspecific differences in inclination to improvise during the execution of a given trajectory.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Aguilar-Argüello et al. (2019).

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